

Ecophysiology

Moderator:

MARY ANN SWORD

USDA Forest Service

WATER RELATIONS AND GAS EXCHANGE OF LOBLOLLY PINE SEEDLINGS UNDER DIFFERENT CULTURAL PRACTICES ON POORLY DRAINED SITES IN ARKANSAS

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Abstract—Substantial forest acreage in the south-central U.S. is seasonally water-logged due to an underlying fragipan. Severely restricted drainage in the non-growing season leads to a reduced subsoil zone, which restricts root respiration. The same sites may also be subjected to summer drought. These climatic and edaphic problems may result in low seedling survival and reduced growth. To address these issues, we established ten research sites in southern Arkansas. Six sites in an incomplete factorial design were established in 1999, each with four bedded treatments: 1) control (no subsequent treatment), 2) fertilized during the first two years after planting, 3) complete weed control until canopy closure, and 4) complete weed control and continuous fertilization as per foliar analysis; and two non-bedded treatments: 1) control and 2) fertilization and complete weed control in the first year. Water relations data (diurnal water potential, stomatal conductance, and transpiration) and net CO₂ assimilation were collected during the 1999 and 2000 growing seasons. This paper will include data from the 2000 growing season. Results to date show improved water relations and gas exchange from intensive culture.

INTRODUCTION

There is a substantial acreage of seasonally wet, somewhat poorly drained sites in the Western Gulf. These sites experience standing water through much of the winter due to an underlying fragipan. This results in an anaerobic atmosphere for roots and subsequent poor seedling survival. The condition may also assist in nutrient leaching loss to the subsoil fragipan. The sites also experience summer drought which may contribute to reduced growth. Mechanical site preparation and early cultural treatment can affect pine growth on flatwoods (Lauer and Glover 1998, Shiver and Rheney 1990). Therefore, our research objectives was to test the efficacy of several cultural practices for ameliorating adverse site conditions.

MATERIALS AND METHODS

The research was designed to investigate three treatment factors: mechanical site preparation, fertilization and chemical vegetation control. Treatments tested in an incomplete factorial design were: two levels of mechanical site preparation (no preparation, and bedded and ripped), three levels of chemical vegetation control (no control and chemical control during the first year, and complete vegetation control until canopy closure), and three levels of fertilization (none, fertilization during the first year, and continuous fertilization until desired nutrient foliar concentration was achieved). Six of the 18 possible treatment combinations were established at each of six sites in southern Arkansas:

- Bedding control (BED-N)
- Bedding + complete chemical vegetation control (BED-CV)
- Bedding + continuous fertilization (BED-F)
- Bedding + complete chemical vegetation control + continuous fertilization (BED-CVF)
- Flatplanting control (FP-N)
- Flatplanting + chemical vegetation control in the first year + fertilization in the first year (FP-VF)

Spacing was uniform in any site, but varied among sites to 1.8-2.4 meters between trees on the row/bed and 3.3-4.0 meters between rows/beds. All sites were planted with loblolly pine (*Pinus taeda* L.) in January 1999. A whole plot was 13 rows X 18 trees, of which the central 7 rows X 10 trees were used for measurement giving a three-row buffer on each side and a four-tree buffer on each end. The whole plot covered an area of about 0.40 hectare.

Mechanical Site Preparation

All sites were initially prepared by shearing and burning, followed by a combination plow with a ripping tine and bedding disks, except for the non-bedded plots.

Fertilization

Fertilized plots were treated in a broadcast manner with 280 kilograms per hectare of diammonium phosphate, 140 kilograms per hectare of potassium chloride, and 112

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Table 1—Soil volumetric moisture content ($\text{cm}^3 \text{cm}^{-3}$) of six treatments, bedded (BED) and flatplanted (FP), treated with fertilizer alone (F), complete vegetation control (CV), complete vegetation control and continuous fertilization (CVF), vegetation control and fertilization during year of planting (VF), and control or check (N). Numbers followed by the same letter within columns are not statistically different ($\alpha = 0.05$)

Site	PrepTreatment	June 8	August 18
FP	N	6.9 c	4.9 c
FP	VF	9.8 a	8.0 a
BED	N	6.7 c	4.1 d
BED	F	6.2 c	4.1 d
BED	CV	10.3 a	7.1 b
BED	CVF	8.2 b	5.5 c

kilograms per hectare of a mix of calcium, magnesium, boron, and manganese.

Chemical Vegetation Control

All plots to be treated with herbicide were sprayed with glyphosate and sulfometuron in 1999 and imazapyr and sulfometuron in 2000. Herbicides were applied with backpack sprayers at recommended rates. To ensure a complete vegetation control, plots were resprayed as necessary.

Data Collection

Data were collected throughout the 1999 and 2000 growing seasons. Volumetric soil moisture content was determined using time-domain reflectometry during sampling sessions for water relations at three different locations within each plot at all measurement hours. Diurnal water potential data were collected using a pressure bomb apparatus on three seedlings per plot at 0900, 1200, 1500 and 1800 hours. The same seedlings were used for all measurement hours and also for other measurements such as stomatal conductance, transpiration and vapor pressure deficit, which were measured using a LiCor 6200. In addition, net CO_2 assimilation rate, intercellular CO_2 concentration and incoming irradiance were measured using a LiCor 6250 for the same seedlings concurrent with the other measurements.

RESULTS AND DISCUSSION

Data will be presented from one of the six sites measured, that being located near Crossett. The soil series there is a Calloway silt loam, a fine-silty, mixed, active, thermic Aquic Fragiudalf. The depth of the subsoil fragipan ranges between 50 and 60 centimeters. Data were collected on two 2000 sampling sessions, once at the beginning of the summer (June 8) and again at the end of the summer (August 18). Air temperatures, averaged throughout the day, for these two sampling sessions were 34.8 and 35.1 °C, respectively. Cumulative precipitation for the 14 days preceding June 8 was 6.68 centimeters of which 5.41 centimeters fell in the previous seven days. There was no

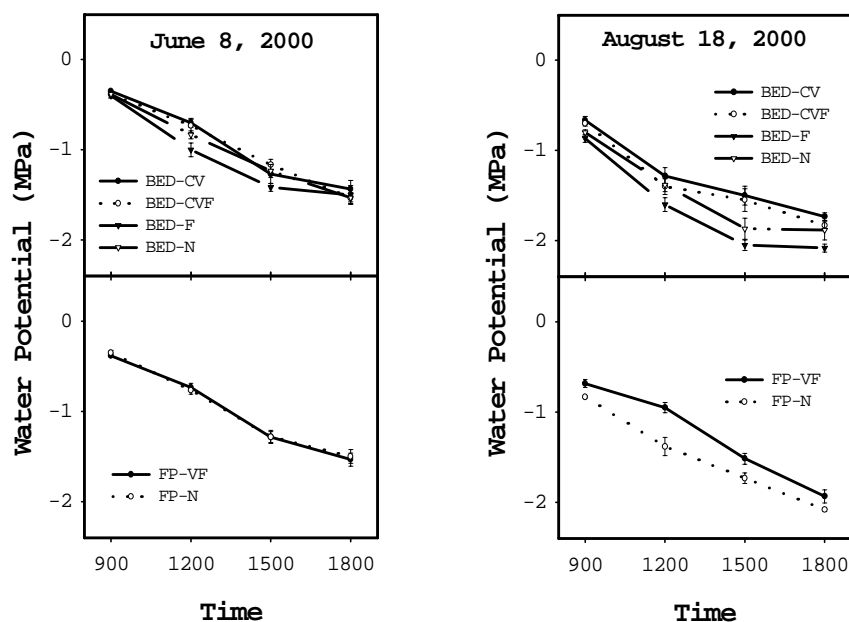


Figure 1—Needle water potential of loblolly pine seedlings during two sampling sessions from four different treatments on bedded plots: control (BED-N), continuous fertilization (BED-F), complete vegetation control (BED-CVF), and complete vegetation control and continuous fertilization (BED-CVF); and two flat-planted plots: control (FP-N) and fertilization and weed control in year of planting (FP-VF). Vertical bars indicate one standard error on each side of symbol.

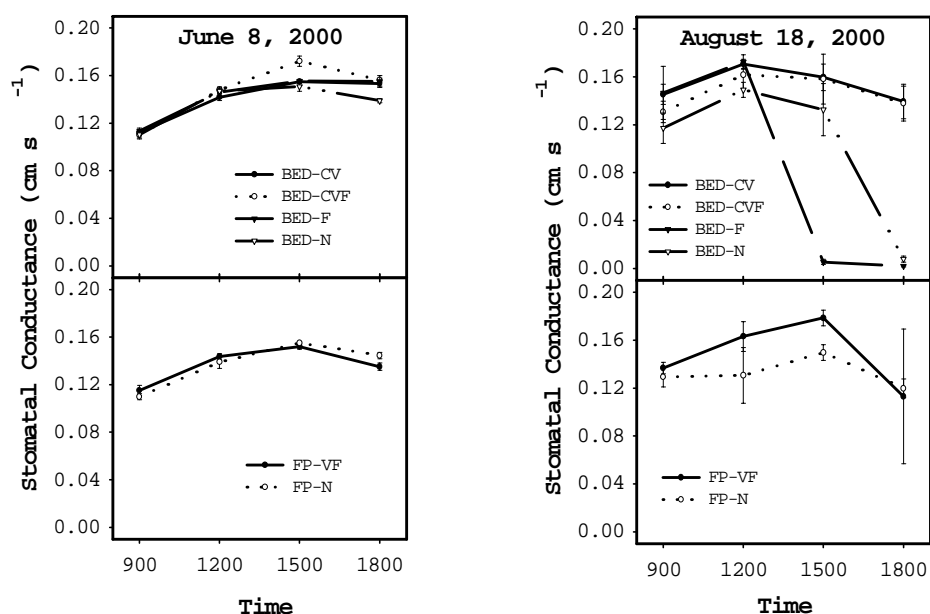


Figure 2—Stomatal conductance of loblolly pine seedlings during two sampling sessions from four different treatments on bedded plots: control (BED-N), continuous fertilization (BED-F), complete vegetation control (BED-CVF), and complete vegetation control and continuous fertilization (BED-CVF); and two flat-planted plots: control (FP-N) and fertilization and weed control in year of planting (FP-VF). Vertical bars indicate one standard error on each side of symbol.

rainfall in the four days immediately preceding data collection. There was no rainfall recorded in the 14 days preceding the August 18 sampling session.

Volumetric Soil Moisture Content

Soil volumetric moisture content was higher for all plots with chemical vegetation control (table 1). There was more water available on June 8 for all treatments than on August 18, reflecting prolonged drought as summer progressed. Bedding decreased soil water availability in summer as there was less water available in the bedded treatments than in flatplanted treatments. For example, soil volumetric moisture content on August 18 for the flatplanted-continuous vegetation control-fertilized treatment was 8.0 percent, whereas for the same treatment on a bedded plot it was only 5.5 percent. Although bedding can enhance early seedling survival, it can also decrease soil water availability during summer drought from enhanced subsoil drainage. Fertilization also affected soil volumetric moisture content when combined with certain site preparation and herbicide treatments (table 1). On bedded treatments, fertilized plots had lower volumetric soil moisture contents when competing vegetation was controlled on both sampling dates (BED-CV vs. BED-CVF). However, the combination of complete vegetation control and fertilization increased soil moisture content on flat-planted plots (FP-N vs. FP-VF). Fertilization alone did not affect soil moisture content on bedded plots (BED-N vs. BED-F). These results seem counterintuitive in that fertilization without competition control would be expected to promote prolific herbaceous plant growth with a consequential decrease in soil moisture. Herbicide application would be expected to diminish this effect. However, the opposite results were observed for which no clear explanation can be offered.

Needle Water Potential

Needle water potential on June 8 was comparable for BED and FP treatments (figure 1). Even though the BED-F treatment had lower water potential at 1200 and 1500 hours compared to the other treatments, it showed comparable water potential at 1800 hours. Needle water potential in the early morning was very high for all treatments and decrease throughout the day linearly, but never went below -1.8 MPa. However, there was a strong treatment difference in needle water potential on August 18. Seedlings from all treatments showed a lower water potential compared to June, starting with a lower early water potential and decreasing to as low as -2.1 MPa at the end of the day, thereby reflecting a moderate to severe water stress (Fitter and Hay 1987, Seiler and Johnson 1988). Seedlings from plots treated with herbicide showed higher water potential indicating that improved plant water relations were obtained from chemical vegetation control by means of increased soil water availability (figure 1).

Stomatal Conductance

Stomatal conductance did not vary between flatplanted plots during the June sampling session (figure 2). On bedded plots, all treatments started to conduct water in a comparable manner early in the day, but seedlings in the BED-N treatment conducted less by the end of the day. Stomatal conductance for all treatments, bedded and flatplanted, increased to a maximum at 1500 hours and then decreased at 1800 hours. There was a strong treatment effect on August 18 on stomatal conductance for all treatments (figure 2). Seedling stomatal conductance for the FP-VF plot was higher for 1200 and 1500 hours than the FP-N. However, the lower stomatal conductance at 1800 hours for FP-VF was due to one sample which

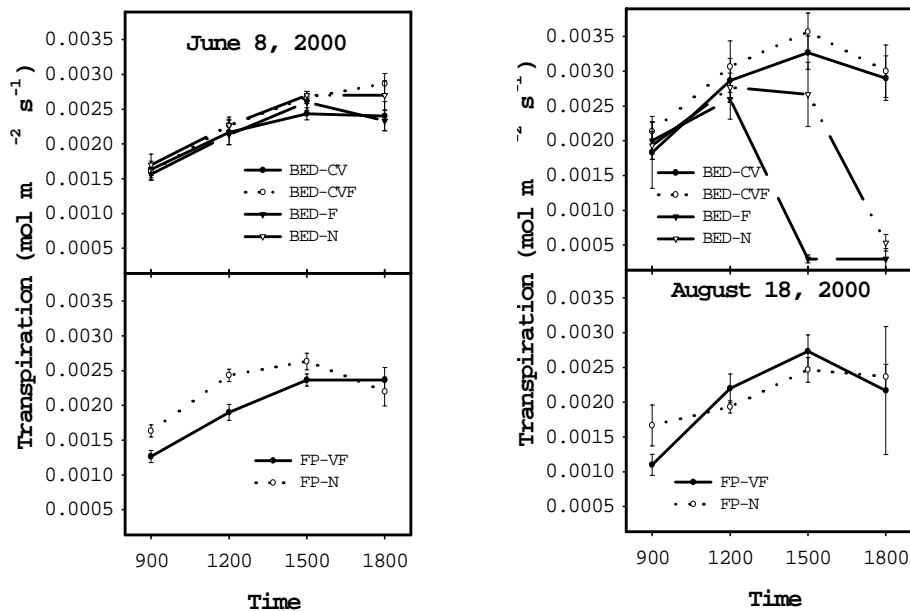


Figure 3—Transpiration of loblolly pine seedlings during two sampling sessions from four different treatments on bedded plots: control (BED-N), continuous fertilization (BED-F), complete vegetation control (BED-CVF), and complete vegetation control and continuous fertilization (BED-CVF); and two flat-planted plots: control (FP-N) and fertilization and weed control in year of planting (FP-VF). Vertical bars indicate one standard error on each side of symbol.

showed stomatal conductance as low as zero presumably due to stomatal closure, resulting in a high standard error for that treatment at that hour. Stomatal conductance for the BED-F ceased after 1500 hours and for BED-N at 1800 hours. Seedlings with water potential lower than -1.8 MPa ceased stomatal conductance.

Transpiration

Transpiration was similar among bedded treatments for most hours on June 8, although there was a treatment difference at 1500 and 1800 hours with BED-CVF transpiring most water (figure 3). Transpiration for the FP-N treatment was significantly ($\alpha=0.05$) higher than for FP-VF until 1500 hours after which it was comparable. Transpiration did not vary between flat-planted treatments on August 18. However, transpiration followed a pattern similar to that for stomatal conductance for bedded treatments on August 18 (compare figures 2 and 3), reflecting that transpiration was controlled by stomatal behavior for this sampling session during this time of severe drought.

Net Photosynthesis

Net CO_2 assimilation rate (i.e., photosynthesis) did not vary between flatplanted plots on June 8, although it varied slightly within the bedded plots with fertilized plots being higher than the N and CV (figure 4). Photosynthesis was strongly affected by stomatal behavior on August 18 when

treatments with no stomatal conductance showed no net CO_2 assimilation; BED-FP after 1500 hours and BED-N after 1800 hours (compare figures 2 and 4).

CONCLUSIONS

There was a strong influence of treatments on seedling water relations and photosynthesis. This was more obvious in the late summer after a droughty summer. Chemical vegetation control played a key role in maintaining improved seedling water relations. However, fertilization helped to enhance net CO_2 assimilation and at a time of severe water stress, there was a continuing CO_2 assimilation due to reduced competition from chemical vegetation control. Even though bedding did result in decreased soil water availability later in the growing season, comparable water relations between seedlings on bedded and flatplanted sites suggest increased root growth in seedlings on bedded plots.

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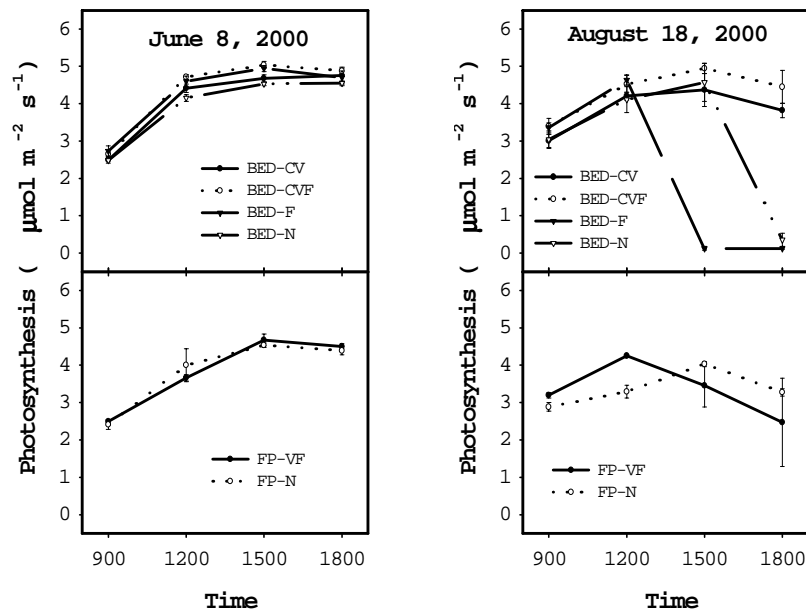


Figure 4—Net CO₂ assimilation (photosynthesis) of loblolly pine seedlings during two sampling sessions from four different treatments on bedded plots: control (BED-N), continuous fertilization (BED-F), complete vegetation control (BED-CVF), and complete vegetation control and continuous fertilization (BED-CVF); and two flat-planted plots: control (FP-N) and fertilization and weed control in year of planting (FP-VF). Vertical bars indicate one standard error on each side of symbol.

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GPP IN LOBLOLLY PINE: A MONTHLY COMPARISON OF EMPIRICAL AND PROCESS MODELS

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Abstract— Monthly and yearly gross primary productivity (GPP) estimates derived from an empirical and two process based models (3PG and BIOMASS) were compared. Spatial and temporal variation in foliar gas photosynthesis was examined and used to develop GPP prediction models for fertilized nine-year-old loblolly pine (*Pinus taeda*) stands located in the North Carolina Sandhills. Foliar gas exchange in both the upper and lower thirds of crowns was monitored monthly for a year. Based on these data, empirical models were developed for the growing and non-growing seasons and upper and lower crown levels. Common empirical models include the variables photosynthetically active radiation (PAR), Ln(PAR), and VPD. Statistical differences in model estimates for crown positions and for both the growing and non-growing seasons indicated that the use of separate empirical models was appropriate for GPP estimations, yet simulated light-response curves yield similar rates. Monthly GPP estimates derived from empirical models were compared with process model predictions. Average monthly environmental data were applied to models to estimate GPP. Both process models predicted a greater relative GPP during the growing season (80 percent) compared with the empirical model (65 percent), while the opposite trend was apparent for the non-growing season. Monthly GPP variability was greater in the 3PG and BIOMASS predictions, appearing to reflect monthly temperatures and stand growth, while the empirical analysis predicted a relatively high contribution to yearly GPP during the non-growing season. Predicted GPPs for the entire year were 192.8, 142.8, and 192.4 mol C/m² for the empirical, BIOMASS, and 3PG models, respectively.

INTRODUCTION

Gross primary productivity (GPP) is a measure of the potential carbon gain by a stand prior to respiratory losses. GPP can not be measured directly and therefore must be estimated using models developed to predict the total carbon yield or biomass accumulation prior to respiration. Process models have become increasingly important and useful in assessing stand productivity since they integrate several biological functions that directly define the growth potential of a tree and ultimately the stand (Johnson and others 2001).

3PG and BIOMASS are photosynthesis-stomatal conductance process models, which integrate physiological plant responses, ecological processes, and physical relationships within the stand to predict stand growth. Both have been calibrated for loblolly pine. 3PG and BIOMASS primarily utilize quantum efficiency and maximum carbon assimilation rate (A_{max}) to predict carbon fixation rates. An extensive overview of 3PG and BIOMASS is provided by Landsberg and others 2001 (3PG), Landsberg and Waring 1997 (3PG), McMurtie and Landsberg 1992 (BIOMASS). Solar radiation, atmospheric vapor pressure deficit (VPD), rainfall, frost days per month, and average temperature are

input drivers used in 3PG calculations. Additionally, a fertility rating is used to adjust the simulated photosynthesis light-response curve in 3PG. BIOMASS uses shortwave radiation, VPD, minimum and maximum daily temperatures, and precipitation. BIOMASS and 3PG essentially calculate GPP based on the amount of absorbed PAR at the canopy level by converting light energy into carbon fixation potential. Other environmental inputs alter the efficiency and rate of carbon fixation at the canopy level.

Process models are rarely evaluated to determine if predicted GPPs reflect actual physiological data collected from a stand. The collection of gas exchange data over an entire year provided the unique opportunity to develop seasonal empirical photosynthesis models that could be used to validate process model GPP outputs. The two objectives of this study were (i) to compare monthly predicted GPP in a loblolly pine stand using two process models (3PG and BIOMASS) and an empirical model developed from gas exchange data collected from the same stand and (ii) to compare total yearly predicted GPP using the same models.

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METHODS

Study Site

Photosynthesis measurements for empirical model development were taken in Scotland County, North Carolina (35°N lat., 79°W long.) at the United States Forest Service (USFS) Southeastern Forest Tree Experiment and Education Site (SETRES). The stand consists of hand planted loblolly pine (2 x 3 m spacing) established in 1985 (14 years old at the beginning of the study). The site is flat, infertile, excessively drained, sandy, siliceous, and composed of thermic Psammentic Hapludult soil (Wakulla series). The average annual precipitation is 121 cm, but drought is common in the summer and early fall. The average summer temperature is 26°C and the winter average is 9°C. The average annual temperature is 17°C. The climate is humid and temperate with hot summers and mild winters, allowing for over a six month growing season. The native forest cover type is Longleaf Pine-Scrub Oak. The established site study design is a 2 x 2 factorial combination of fertilized and irrigated additions replicated four times. The plots consist of 30 x 30 m measurement plots within 50 x 50 m treatment plots. Interaction among below ground matter from adjacent plots is prevented by a 150 cm deep plastic liner that separates plots. Non-pine vegetation is controlled by mechanical and chemical (glyphosate) treatments such that no understory vegetation exists. Nutrient applications began in March 1992 and continued through March 1998. The total amount of each nutrient (in Kg/Ha) added over the six year period is as follows: N (777), P (151), K (337), Ca (168), Mg (164), S (208), and B (3.9). In the fertilized plots, crown closure is common. Total biomass accumulation at SETRES increased 91 percent four years after initial fertilization treatments began (Albaugh and others 1998).

Photosynthesis Measurements

Photosynthesis was measured monthly in fertilized plots from April 1999 to March 2000 at SETRES using the LiCor 6400 Portable Photosynthesis System (LiCor, Lincoln, NE). Fertilized plots were chosen over other treatments because the fertilized stands most closely represent intensively managed loblolly pine forests (since fertilization is common and irrigation is not). Photosynthesis rates from upper and lower crown cut foliage were measured (Ginn and others 1991) from a subsample of 2 trees per block for a total of 16 measurements (4 blocks x 2 crown positions x 2 subsamples). Gas exchange was measured in each block sequentially, and subsamples from each level were chosen randomly for sampling. Blocks were always measured in the same order. This sequence was repeated three times on each measurement day in order to capture an abbreviated diurnal response to daily environmental changes. Measurements included morning (9 AM), afternoon (11:30 AM), and late afternoon (1:30 PM) measurement periods. A total of 48 measurements (three sampling sequences) in fertilized plots were generally taken throughout the day.

Shoots were cut using a pole pruner and measurements were taken immediately on a detached fascicle. All measurements were taken at the ambient temperature and humidity, and CO₂ concentrations were held constant in the

chamber at 350 ppm. The average PAR was estimated for the upper and lower third of crowns and kept constant in the measurement chamber (using the LiCor's actinic source) for each crown level in the block throughout a measurement period. The PAR for each crown level was determined by evaluating the average PAR in full sunlight (for the upper third) and the average PAR in the understory (for the lower third) prior to the measurement period. The PAR was reassessed and adjusted for each measurement period according to the PAR levels immediately prior to sampling. Water potentials were determined for the same branch as the sample immediately after being cut using a field pressure chamber (PMS instrument Co., Corvallis, OR). All measurements were completed in one day. Needle diameter was immediately recorded and leaf area was later determined using the following equation (Ginn and others 1991):

$$LA_i = (n * l * d) + (p * d * l)$$

where l = the length of the needle, d = fascicle diameter and n = number of needles in the fascicle. Values were adjusted to represent gas exchange on a per leaf area basis. Foliar nitrogen percentages of measured needles were obtained from pooled samples collected from each block/crown position combination during eight of the twelve months using a Carla ERBA (Raleigh, NC).

Empirical Model Development

Empirical models were developed using multiple linear regression techniques in SAS[®]. (SAS Statistical Institute, Cary, NC). Common simplified gas exchange models for crown positions were developed for the growing (April – October) and non-growing (November – March) seasons. Common models include the variables PAR, $\ln(\text{PAR})$, and VPD. Air temperature, stem water potential, relative humidity, and foliar nitrogen contents were not significant model variables. Statistical comparisons of seasonal and crown position model parameter estimates revealed that significant differences exist among all models. Therefore, models for the upper and lower crowns within the growing and non-growing seasons were used to estimate GPP.

GPP Analysis

Monthly GPP was predicted using the empirical models, 3PG, and BIOMASS. 3PG was originally calibrated for loblolly pine at SETRES (Landsberg and others 2001). Average environmental data for a 20-year period at SETRES was used to calculate GPP in 3PG, while BIOMASS utilized 1995-1996 environmental data from SETRES. 3PG outputs data in a monthly time-step while BIOMASS provides a daily time-step output. Daily BIOMASS outputs were summed for each month. Upper and lower PAR and leaf area index (LAI) for three canopy layers were estimated using BIOMASS. The middle layer was divided in half and added equally to both the upper and lower layers for the empirical estimates of GPP.

RESULTS AND DISCUSSION

Actual mean monthly photosynthesis measured at SETRES remained relatively high during the non-growing season with significantly greater rates occurring in the upper crown compared to the lower crown during all

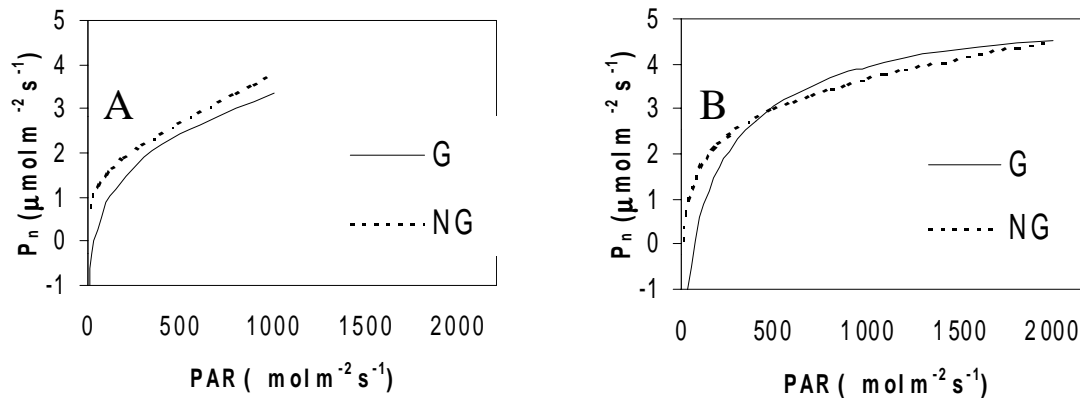


Figure 1—Simulated light response curves for the lower crown (A) and the upper crown (B) for both the growing and non-growing seasons.

months ($p < 0.05$) (figure 1). Mean rates in January and February were higher than those recorded in June and largely reflect the cloudy conditions on the June measurement day. High photosynthesis rates at SETRESII (an adjacent sister experimental station) have been recorded during the non-growing season as well (unpublished data).

As mentioned before, statistical tests revealed that significant differences exist among parameter estimates of photosynthesis prediction models developed for the growing and non-growing seasons and the upper and lower crowns (table 1). However, predicted light response curves for the growing and non-growing seasons within a crown level are similar, implying that the photosynthetic response to light and the ability to fix carbon does not greatly differ with season (figure 2). This is reflected in the monthly empirical GPP predictions for the upper and lower crowns (figure 3), which suggest that GPP is reduced by only a third in the winter months relative to the peak July

rate. Monthly BIOMASS predictions exhibit a lower relative GPP accumulation during the winter months and a greater accumulation during the growing season (figure 4A), suggesting that BIOMASS is sensitive to low temperatures. This is reflected in daily BIOMASS outputs in which a GPP of zero was predicted for days below freezing (data not shown). 3PG predicts a rapid increase from January through May, followed by more erratic monthly values (figure 4B). This behavior is primarily due to the density induced mortality function incorporated into the process model (Landsberg and others 2001).

The BIOMASS and 3PG models predict that 80 percent of the yearly GPP accumulates during the growing season and 20 percent accumulates during the non-growing season. The empirical model predicts that 65 percent and 35 percent of the GPP is distributed between the growing and non-growing seasons, respectively (figure 5A).

Table 1—Significant variables, Parameter estimates, and total R^2 values for common photosynthesis prediction models developed for the upper and lower crowns and the growing and non-growing seasons in fertilized stands at SETRES. All parameter estimates were statistically different ($p < 0.1$)

Lower Crown			Upper Crown		
Growing Season					
Parameter	Estimate	R ²	Parameter	Estimate	R ²
Intercept	-1.802	0.59	Intercept	-5.542	0.60
PAR	7.237 x 10 ⁻⁴		PAR	5.477 x 10 ⁻⁴	
Ln(PAR)	0.7912		Ln(PAR)	1.653	
VPD	-0.5238		VPD	-0.6983	
Non-Growing Season					
Intercept	-0.4707	0.63	Intercept	-2.048	0.62
PAR	0.001816		PAR	3.670 x 10 ⁻⁴	
Ln(PAR)	0.2684		Ln(PAR)	0.7066	
VPD	0.2911		VPD	0.2356	

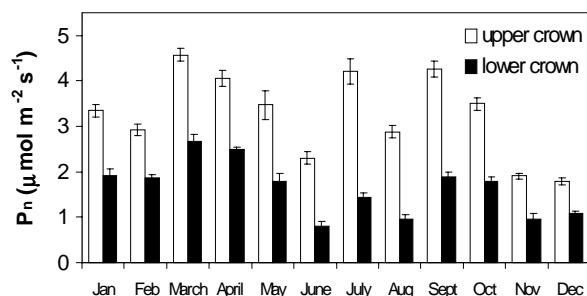


Figure 2—Mean monthly photosynthesis rates for 1999-2000 measurements in upper and lower crown foliage at SETRES. Photosynthesis was significantly greater in the upper crown for all months ($p < 0.1$).

Absolute predicted GPPs during the growing season are fairly similar for the empirical model and BIOMASS (about 120 mol C/m²), while 3PG predicts a much higher value (160 mol C/m²) (figure 5B). During the non-growing season, both 3PG and BIOMASS predict lower actual values compared with the empirical model. Thus, in relative terms (figure 5A) the process models may overpredict GPP during the growing season and underpredict GPP during the non-growing season. In absolute terms (figure 5B), only 3PG predicts greater GPP during the growing season when compared with the empirical predictions. 3PG is calibrated using field growth and biomass measurements; therefore, the model may not accurately account for the potential carbon gain in the winter if photosynthate does not immediately contribute to growth. Evidence exists that labile carbon pools accumulate in loblolly pine during the winter and are utilized during high stress situations in the summer when carbon fixation is limited and does not meet the metabolic or growth requirements of the tree (Sampson and others 2001).

Thus, winter GPP may not result in immediate measurable growth. Seasonal 3PG estimates probably more closely

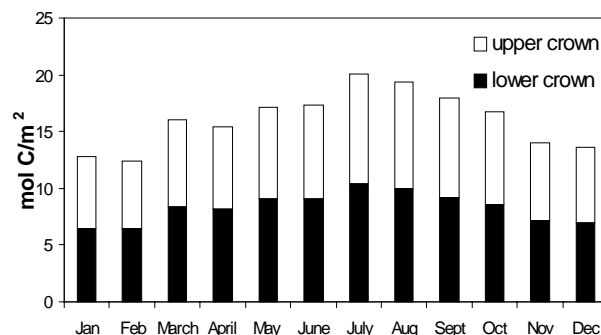


Figure 3—Empirically derived predictions of monthly GPP in the upper and lower crowns.

parallel growth data while the empirical analysis directly reflects carbon fixation estimates. This is consistent with growth data collected from SETRES in which a majority of measurable stem wood production is observed during the growing season (unpublished data).

Interestingly, the cumulative predicted GPPs for the year are fairly similar among the empirical (192.8 mol C/m²), BIOMASS (142.9 mol C/m²), and 3PG (192.4 mol C/m²) models. Again, 3PG was calibrated for loblolly pine at SETRES, which is where data was collected for empirical model development. This may explain why the yearly total is similar for the two models since 3PG was calibrated against actual field biomass data and the empirical model is likely a good estimate of GPP based on actual physiological measurements of carbon fixation on the site over a year. 3PG and the empirical models used different data collected at SETRES and represent two modeling approaches. The fact that they arrive at similar cumulative predicted GPPs validates both models on a yearly scale.

These results indicate that the process models do not fully account for winter acclimation and summer declines. 3PG

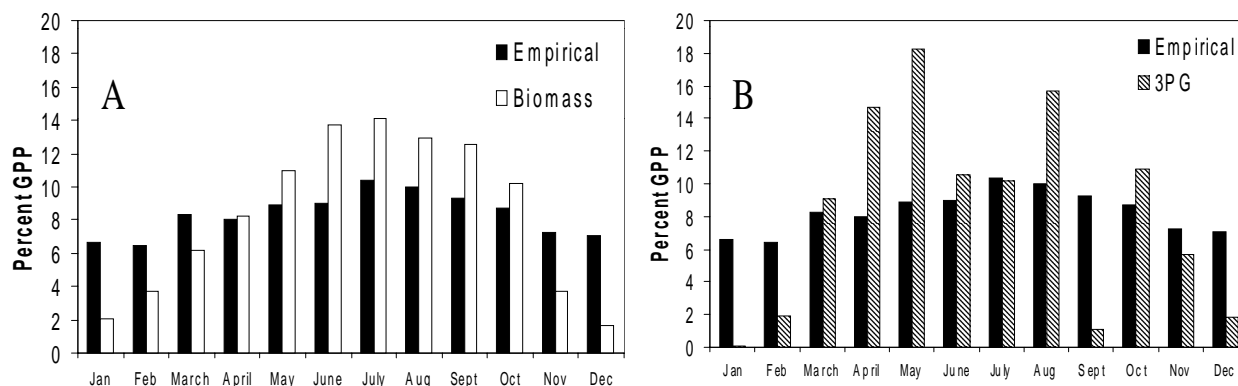


Figure 4—Percent monthly GPP contributions relative to yearlong totals for empirical and BIOMASS predictions (A) and empirical and 3PG predictions (B).

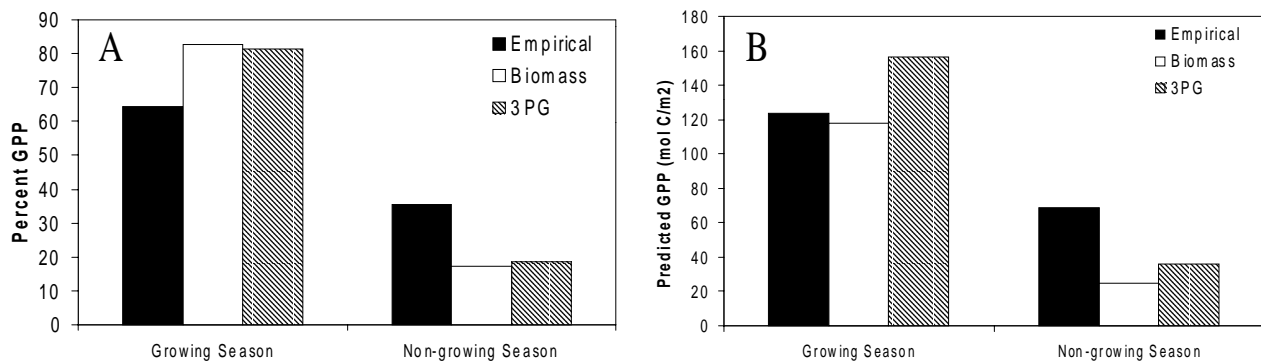


Figure 5—Empirical, BIOMASS, and 3PG estimates of percent GPP contribution (A) and actual predicted GPP (B) for the growing (April-October) and non-growing (November-March) seasons.

and BIOMASS have critical temperature thresholds (Landsberg and others 2001 (3PG), McMurtie and Landsberg 1992), which may result in oversensitivity when the environmental data are averaged, especially when average temperatures are skewed by a few instances of extremely low or high temperatures. During the summer, higher predicted GPPs by process models relative to the empirical model could be explained by a lower sensitivity to VPD. The empirical estimates show approximately a 25 percent decline due to high VPDs in the summer (figure 6), which is similar to the actual difference in predicted GPPs between the empirical and process models during the growing season (figure 5B).

The empirical approach to predicting GPP provides reasonable estimates - at least for SETRES. Scaling up of the empirical model to the stand level at other locations may possibly be achieved by taking into account factors that drive total carbon fixation and ultimately GPP. LAI is an excellent indicator of potential productivity (Teskey and others 1987, Teskey and others 1994, Vose and Allen 1988) and highly reflective of site fertility (Gillespie and others 1994, Albaugh and others 1998). Reported crown leaf area estimates for loblolly pine in Hawaii were five times greater than stands examined in coastal South Carolina at 25 years (Harms and others 1994). Greater crown leaf areas paralleled higher total biomass estimates

in Hawaiian loblolly pine. Therefore, leaf area may be an excellent indicator of site productivity and substitute for fertility ratings that are required inputs in process models and are often difficult to determine (Landsberg and others 2001). Leaf area is directly related to GPP since total crown carbon fixation is enhanced with the increase in photosynthetic machinery. This of course is only the case when the assumption is made that greater fertility does not directly affect the photosynthetic capacity or efficiency of an individual leaf. Incident radiation and day-length, and density-induced mortality would also have to be accounted for in order to expand the inference space of empirical estimates to include other sites.

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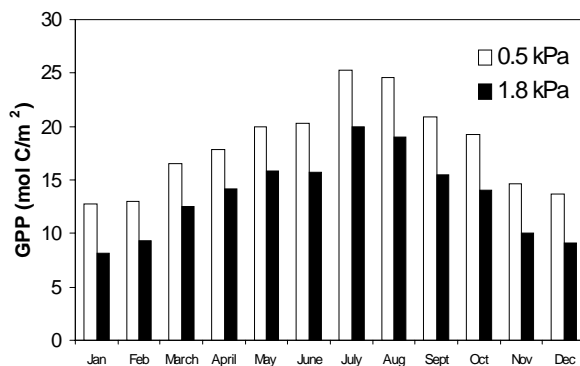


Figure 6—The effect of high and low VPD on empirically predicted GPP. The selected VPDs represent the high and low monthly averages recorded at SETRES.

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FAMILY DIFFERENCES IN ABOVEGROUND BIOMASS ALLOCATION IN LOBLOLLY PINE

Scott D. Roberts¹

Abstract — The proportion of tree growth allocated to stemwood is an important economic component of growth efficiency. Differences in growth efficiency between species, or between families within species, may therefore be related to how growth is proportionally allocated between the stem and other aboveground biomass components. This study examines genetically related differences in aboveground biomass allocation in loblolly pine. I destructively sampled 58 trees from seven families selected to represent differences in growth rate (fast vs. slow) and crown size (large vs. small). The 15-year-old trees were all planted on the same site at the same spacing. Relative allocation to stem, foliage, and branch wood, and the ratio of foliage biomass to total crown biomass, were examined as a function of the logarithm of DBH. Large-crowned trees, compared to small-crowned trees of similar DBH, differed significantly in percent of total aboveground biomass allocated to the stem and to branch wood. Small-crowned families generally allocated proportionally less biomass to branch wood and more to the stem across the range of tree sizes examined. Relative allocation to foliage biomass did not differ, although lower allocation to branch biomass in small-crowned trees resulted in a significantly greater ratio of foliage to total crown biomass. Comparing trees from fast- and slow-growing families, only relative allocation to foliage differed significantly, although a strong interaction between DBH and growth characteristic made interpretation of the relationship difficult. These results suggest that families do differ in relative aboveground allocation, but these differences may not be related to family differences in stemwood productivity.

INTRODUCTION

A primary emphasis in silviculture is the management and control of tree growth. Total tree growth is a function of how much foliage is contained in the crown, the average photosynthetic rate of that foliage, and the efficiency in which the tree converts fixed carbohydrates into biomass. Of commercial importance is how much of that biomass, or growth, is converted to stemwood. Thus, how biomass is allocated within the tree plays an important role in forest productivity. Being able to manipulate growth allocation is one way that forest production can be improved. Allocation patterns in trees have been shown to vary with tree age, nutrient or water availability, and with stand density under which the tree develops.

Genetics also influence the proportion of growth allocated to useable portion of the plant, or harvest index (Dickmann 1985). Several analyses have suggested that genotypes promoting narrow, sparsely branched crowns lend themselves to greater growth efficiency (stem growth per unit leaf area) (Kärki and Tigerstedt 1985, Kuuluvainen 1988). However, studies specifically examining genetic differences in allocation patterns in trees, including examinations of southern pines, have had mixed results.

Seedling studies have often suggested genetic differences in allocation patterns. Li and others (1991), working with 1st-year seedlings of 23 loblolly pine families, found family differences in relative biomass allocation between root and shoot and between needles and stem. Bongarten and

Teskey (1987) compared growth partitioning among 1-yr-old loblolly pine seedlings from seven seedlots of diverse geographic origin and found seedlot differences in relative allocation between root, stem, and foliage. However, these differences were not strongly related to differences in productivity. It is also not clear whether allocation differences observed in seedlings will be maintained in older stands.

Studies on older trees have been more equivocal, not always showing clear differences in allocation patterns. Pope (1979) examined 11-yr-old trees from four loblolly pine families, all selected for fast growth. The families differed in total production, but not in relative allocation patterns. Conversely, Matthews and others (1975) found family differences in the proportional distribution of woody biomass to the stems in 8-yr-old Virginia pine. Cannell and others (1983) reported that clones displaying sparse branching of both Sitka spruce and lodgepole pine were more efficient stemwood producers.

Commercial agriculture has exploited genetic differences in growth allocation to greatly increase crop yields. Forestry, however, while making some gains, has yet to take full advantage of these opportunities; and in fact has yet to establish a conclusive correlation between genetic differences in growth allocation and productivity. My objectives in this study were to determine if genetic differences in aboveground carbon partitioning could be observed in 15-year-old loblolly pine. If genetic differences were observed, I wanted to determine if these differences were related to family differences in productivity.

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Table 1—Genetic characteristics and size distribution of 58 destructively sampled 15-year-old loblolly pine

Type		D. B. H.(cm)		Height (m)			
Family	n	Growth	Crown	Mean	Range	Mean	Range
NC1	8	Fast	Small	18.7	14.7-22.1	17.5	16.0-18.8
NC8	8	Fast	Small	19.8	15.8-23.5	17.2	15.4-18.5
NC4	9	Fast	Large	18.8	12.6-24.3	16.7	14.0-18.0
NC3	8	Slow	Small	19.2	12.4-23.3	16.4	13.8-18.0
NC6	8	Slow	Small	17.2	14.5-19.4	16.7	16.0-18.0
NC2	9	Slow	Large	20.1	15.8-25.3	16.2	14.4-17.5
NC5	8	Slow	Large	18.1	11.6-22.5	16.6	13.8-18.0
ALL	58			18.9	11.6-25.3	16.7	13.8-18.8

METHODS

This study was conducted on Mississippi State University's John Starr Memorial Forest located in Winston County, MS (33°16'N, 88°52'W). The soils on this interior flatwood site are a Glossic Fragiudult (Prentiss loam) with a fragipan at a depth of approximately 0.5 to 0.8 m. Average annual temperature is ca. 17.2°, and average annual precipitation is ca. 1375 mm. Site index at base age 25 for loblolly pine is approximately 23 m.

Fifty-eight 15-year-old loblolly pine trees were destructively sampled in August 1999. The trees were open-pollinated progenies of seven North Carolina families selected from an industrial tree improvement program. Families were selected to represent combinations of fast vs. slow growth rate, and large vs. small crowns. The trees were all from a single block that had been planted in family rows on a 1.5m x 3.0m spacing. Trees ranged in size from 11.6 cm to 25.3 cm DBH (table 1). An eighth family and an unimproved check were excluded from this analysis because they were planted as border rows. A more complete description of the families is provided by Land and others (1991).

Height and DBH of each tree was measured before felling. After felling, each tree was separated into aboveground biomass components – stem (including bark), branches, and foliage with subtending twigs. Each component was weighed fresh in the field, and a subsample was weighed fresh and retained for further analysis. In the laboratory, subsamples were dried at 80°C to a constant weight and weighed to determine a fresh weight:dry weight ratio. Foliage was removed from twigs to determine a foliage weight:wood weight ratio. Using these ratios, a total dry weight for stemwood, branchwood, and foliage was determined for each tree.

Analysis to determine genetic differences in relative aboveground biomass allocation was based on the relationship between percent allocation to each biomass component and stem DBH. This accounted for the changes in biomass allocation that occur as trees get larger. Log-transformed values of DBH were used to account for the nonlinear nature of the relationships. Standard analysis of covariance procedures were employed to test for genetic differences, using the GLM procedure in SAS. Significance was accepted at a P-value ≤ 0.10 .

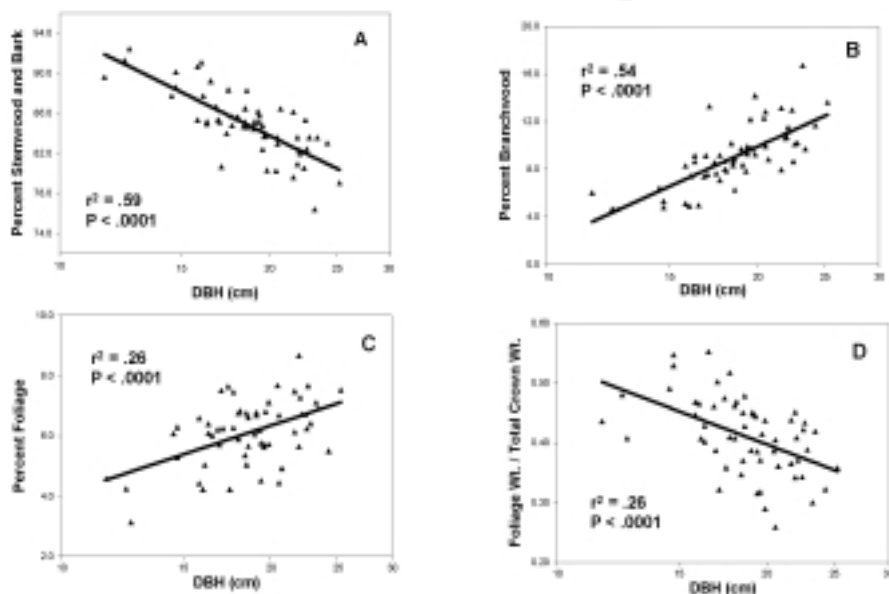


Figure 1 — Log-linear relationships between stem DBH and percent of aboveground biomass allocated to (A) Stemwood and Bark, (B) Branchwood, and (C) Foliage. (D) shows the relationship between DBH and the ratio of foliage weight to total crown weight

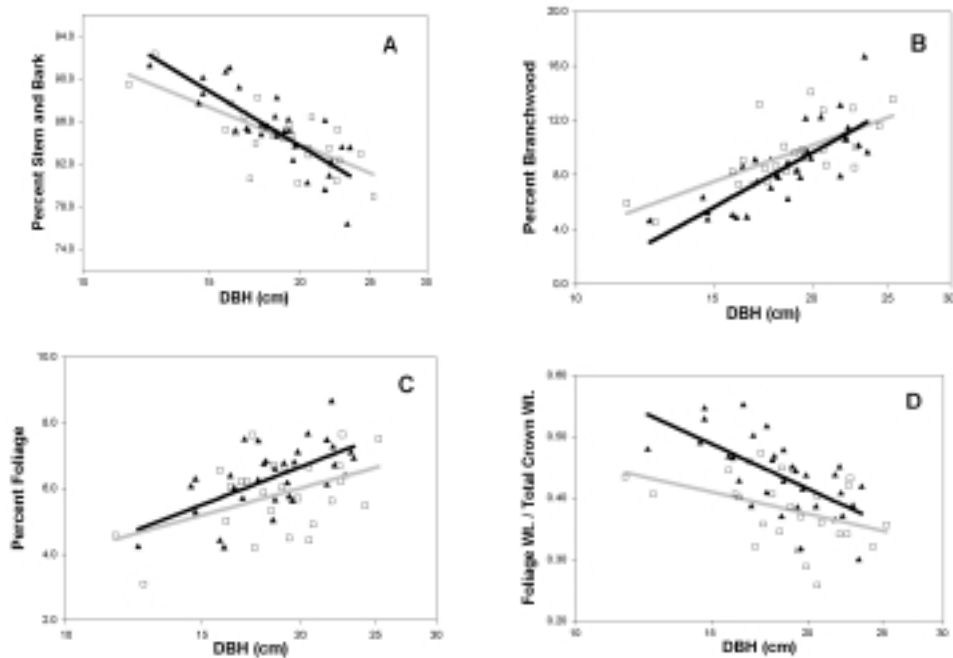


Figure 2 — Comparison of relative biomass allocation patterns between trees from small-crowned families (black triangles, black line) and trees from large-crowned families (gray squares, gray line). Differences in allocation to Stem (A) and Branchwood (B) are statistically significant. Differences in allocation to Foliage (C) are not significant. Differences in Foliage Ratio (D) are statistically significant.

RESULTS

The relationships between relative allocation to each of the biomass components and the logarithm of DBH across all 58 trees were all highly significant. Relative allocation to stemwood decreased as trees got larger (figure 1A), while allocation to both branches and foliage (figure 1B & 1C) increased with tree size. In addition, the ratio of foliage weight to total crown weight decreased as trees got larger (figure 1D). This foliage ratio has been used to help explain the decrease in leaf area efficiency (stem growth / LA) that

has often been observed as mean crown size (leaf area per tree) increases (Roberts and Long 1992).

Reduced allocation to the stem and increased allocation to the crown as trees get larger is a common observation that illustrates the influence of normal developmental processes. Considerable variation exists in these relationships, however. Some of this variation might be explained by family differences in allocation patterns. However, when family was

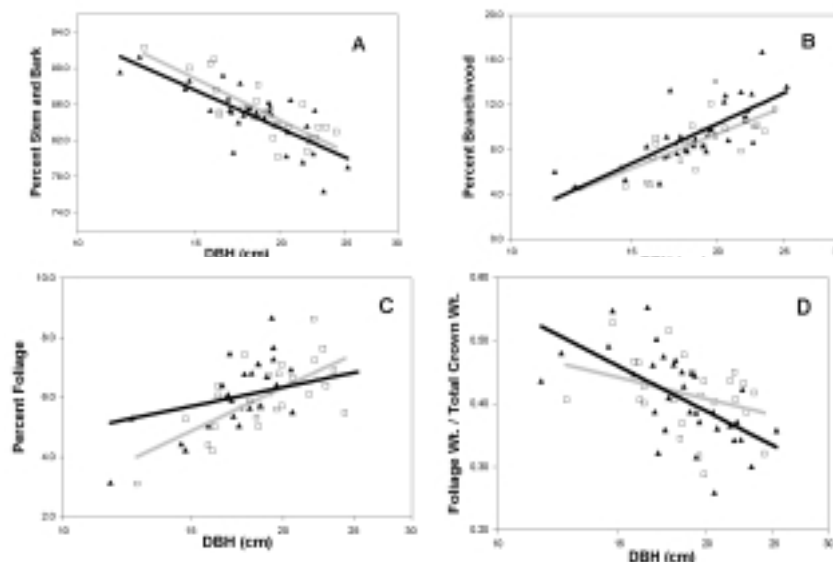


Figure 3 — Comparison of relative biomass allocation patterns between trees from fast growing families (gray squares, gray line) and trees from slow growing families (black triangles, black line). Differences in allocation to Stem (A) and Branchwood (B) are not statistically significant. Differences in allocation to Foliage (C) are statistically significant. Differences in Foliage Ratio (D) are not statistically significant.

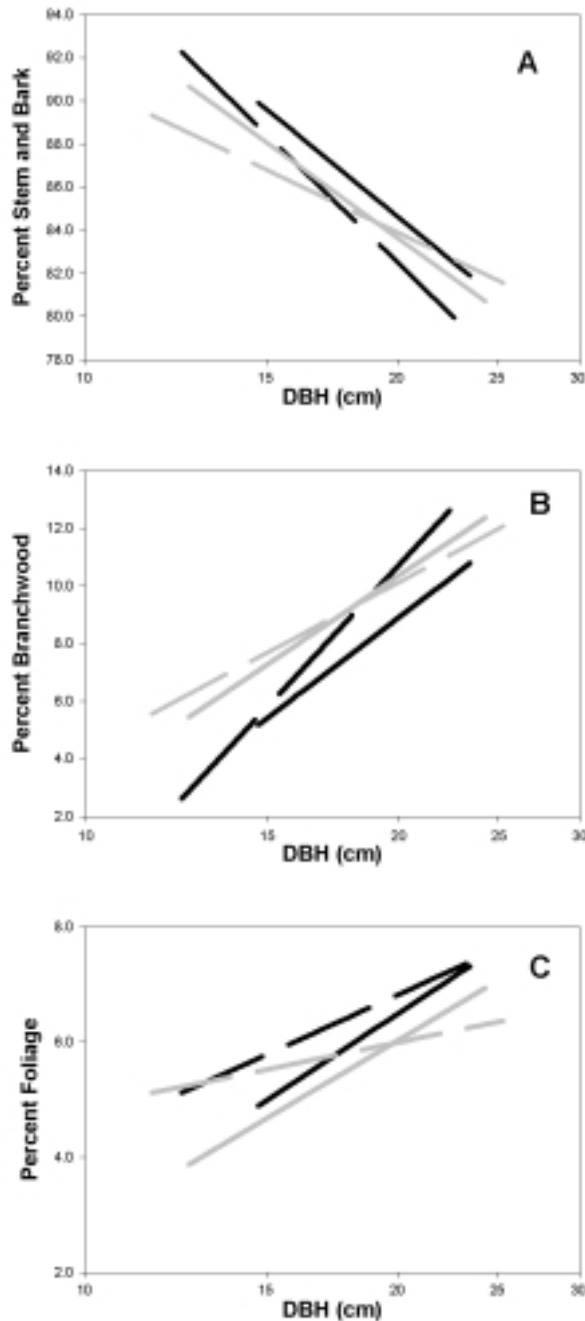


Figure 4 — Comparison of relative biomass allocation patterns between tree “types” representing combinations of crown size and growth rate. Solid black line = fast growing, small crown. Solid gray line = fast growing, large crown. Dashed black line = slow growing, small crown. Dashed gray line = slow growing, large crown. Type is statistically significant in explaining percent allocation to Stem (A). Differences in allocation to Branchwood (B) and to Foliage (C) are not statistically significant.

included as a covariate in the analysis, it was not significant suggesting that the variability in these relationships could not be explained by individual families.

The trees were separated into two groups of families that had been selected for differences in crown size, and the allocation relationships between these two groups were compared. Relative allocation to the stem differed significantly between the two groups. The slope adjusted mean percent allocation to stemwood was greater for small crowned families than for large crowned families ($P = .08$) (figure 2A), although there was a significant interaction ($P = .08$) between growth rate and log DBH.

Relative allocation to branchwood also differed significantly between the two groups. As might be expected, allocation to branches was greater for large crowned families than for small crowned families ($P = .08$) (figure 2B). The interaction term was again significant ($P = .10$), although when plotted on non-transformed axes, the curves appear to be coming together at higher DBH. This might indicate that the differences in allocation to branches are becoming less as the trees get larger.

Relative allocation to foliage was not significantly different between large and small crowned families ($P = .53$); although mean allocation to foliage was slightly higher for small crowned families (figure 2C). Due to differences in relative allocation to branches, foliage ratio did differ significantly between the two groups ($P = .07$). Families selected for small crowns had a higher ratio of foliage to total crown weight (figure 2D). Again, this could be an indication of greater leaf area efficiency for small crowned families.

The trees were next separated into two groups of families based on differences in inherent growth rate, and the allocation patterns of families selected for fast growth rate were compared to those selected for relatively slower growth rates. Relative allocation to the stem was not significantly different between the two groups ($P = .62$), although on average, fast growing families allocated slightly more to stem (figure 3A). Relative allocation to branches was also not significant ($P = .66$), but again, on average, fast growing families put slightly less into branches (figure 3B). There was a significant difference in the slope adjusted mean for relative allocation to foliage ($P = .06$), although, somewhat counter intuitively, slow growing families appear to allocate slightly more to foliage (figure 3C). However, a significant interaction between the growth term and log DBH ($P = .06$) made this difficult to interpret. Foliage ratio was not significantly different between the groups of fast growing versus slow growing families (figure 3D).

The families were lastly grouped based on combinations of crown size (large vs. small) and growth rate (fast vs. slow), and allocation patterns were compared between the four genetic “types.” Type was statistically significant in explaining variation in relative allocation to stem ($P = .09$), however, the significant interaction ($P = .09$) makes it difficult to separate the

various types in any meaningful way. It is interesting to note, however, that the fast growing/small crowned families generally allocated proportionally more biomass to the stem than the other types (figure 4A) across the range of trees examined.

Genetic type had a P-value of .11 in explaining relative branch allocation, with a P-value of .12 for the interaction between type and dbh. Again, the fast growing/small crowned families separated themselves somewhat from the other types, allocating relatively less biomass to branchwood (figure 4B). Type was not significant in explaining allocation to foliage ($P = .30$), although relative allocation to foliage was again slightly lower for fast/large compared to fast/small (figure 4C).

DISCUSSION

This study is somewhat unique in that the genetic selections included not just families that differed in growth rate, but also families that presumably had inherent differences in allocation patterns, i.e., large vs. small crowns. As expected, there were differences in patterns of biomass partitioning related to selected differences in crown size. For a given tree dbh, families selected for small crowns allocated slightly more to the stem and slightly less to branches. Also, while not statistically significant, small crown families on average allocated slightly more to foliage. Small crowned families also tended to have significantly higher foliage ratios, which could be an indirect indicator of greater leaf area efficiency for small crowned trees. Comparisons among families selected for differences in growth rate showed only relative allocation to foliage differed significantly; and even then, the strong interaction makes interpretation difficult.

This study was limited in the range of tree sizes sampled; although to a certain extent that was a positive in this study. All of the trees developed on the same site, at the same spacing, and under essentially the same competitive environment, thus minimizing some of the developmentally influenced differences in growth allocation.

The results from this study provide support that there are genetic differences in aboveground allocation patterns in loblolly pine. This showed up primarily as differences in allocation between the stem and branches. The data do not statistically support the contention that faster growing families preferentially allocate more of their aboveground growth to the stem and less to the crown. However, while not statistically significant, mean values do suggest the possibility of greater relative allocation to stem in fast growing trees.

The results of this analysis agree with the conclusion of Bongarten and Teskey (1987) that genetic differences in dry matter partitioning do exist in loblolly pine, but that these differences are likely only partially responsible for observed differences in productivity. Other physiological and structural differences between families are sure to have major influences on growth and growth efficiency.

ACKNOWLEDGMENTS

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LAI-2000 ACCURACY, PRECISION, AND APPLICATION TO VISUAL ESTIMATION OF LEAF AREA INDEX OF LOBLOLLY PINE

Jason A. Gatch, Timothy B. Harrington, and James P. Castleberry¹

Abstract—Leaf area index (LAI) is an important parameter of forest stand productivity that has been used to diagnose stand vigor and potential fertilizer response of southern pines. The LAI-2000 was tested for its ability to provide accurate and precise estimates of LAI of loblolly pine (*Pinus taeda* L.). To test instrument accuracy, regression was used to compare needlefall estimates of LAI to those from the LAI-2000. To test instrument precision, analysis of variance was used to test sources of variation including instrument drift, overcast versus clear skies, time of day, and synchronization of above- and below-canopy sensors. A regression model was developed to calibrate visual estimates of LAI with LAI-2000 estimates and measures of height and stand basal area.

INTRODUCTION

Leaf area index (LAI) is the ratio of foliage surface area to ground surface area of a vegetative stand. It has become widely accepted as an indicator of photosynthetic capacity and level of stress of forest stands (Waring 1983). Since maximum LAI of a forest stand is limited by nutrient availability, any deviation from this value can indicate whether it will respond to fertilization, given fixed levels of other growth limiting factors, such as soil water and temperature (Vose and Allen, 1988). Thus, monitoring of LAI has potential application in prescribing of fertilizer treatments.

Techniques for estimating LAI of loblolly pine include those that utilize optical sensors, such as the LAI-2000 canopy analyzer (Li-Cor, Inc., Lincoln NB) and those that are conducted visually (Sampson and others 1996). Estimates from optical sensors are considered reasonably precise and accurate, but they require purchase of expensive equipment. Visual estimates can be reliable and inexpensive, given adequate training of observers, but they can suffer from bias. A combination of the two methods of LAI estimation may provide the desired level of accuracy, precision, and cost. This study had two objectives: 1) to quantify accuracy and precision of the LAI-2000, and 2) to calibrate visual estimates of LAI with LAI-2000 estimates and measures of height and stand basal area.

METHODS

The research was conducted in mid-rotation plantations of loblolly pine that were absent of shrubs and hardwoods. For each test of the LAI-2000, an above-canopy sensor (A) logged readings in a nearby large opening (no vegetation at greater than 15 degrees above the horizon) while a below-canopy sensor (B) was used to log readings within the study area. All LAI-2000 readings were taken with the sensor facing north at 1.4 meters above ground and a 90-degree view cap attached to the lens. In the laboratory, data from the two sensors were merged and LAI was calculated with Li-Cor software.

To test LAI-2000 accuracy, needlefall estimates of LAI were regressed against LAI-2000 estimates using measurements taken at a site near Eatonton GA (Scott 1997). Instrument precision was tested at sites near Athens GA or Phenix City AL by taking repeated measurements above the same points but under different instrument or sky conditions. These tests included comparisons of instrument drift (measurements taken in rapid progression), consecutive days with overcast versus clear skies, time of day (10:30, 11:30, or 12:30 Eastern Standard Time, EST), and levels of synchronization between A and B sensors to identical light conditions (1 percent, 5 percent, and 10 percent differences). Tests of instrument drift, time of day, and A/B sensor synchronization were repeated in March, June, and December 2000. Data from each precision test were subjected to analysis of variance with repeated measurements in time (split-plot design). A blocking factor of either individual sample points within a plot (drift study) or individual plots (time of day and synchronization studies) was included in the design. Linear regression was used to test the relationship between LAI estimates of overcast versus clear skies.

To address the second study objective, a total of 25 points were located in stands that varied in height and stand basal area. Following a period of field training, six observers estimated LAI visually above each point during early May and August 1999 using the methods of Sampson and others (1996). Approximately ten days prior to the visual estimates, LAI of each plot had been estimated with the LAI-2000. Measurements of average height and stand basal area also were taken in each plot. LAI-2000 estimates were regressed against visually estimated values, indicator variables for each observer, and stand variables. Stepwise regression with backward elimination was used to test the significance of each variable in the model.

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RESULTS

Accuracy of the LAI-2000 was high, with estimates exceeding those obtained from needlefall by only 4 percent. No significant differences were found when LAI-2000 measurements were taken in rapid succession above the same points (instrument drift). LAI-2000 readings taken on cloudy days averaged 7 percent greater than those taken on clear days. Readings taken at 10:30 EST averaged 4 percent greater than those taken at 11:30 and 12:30 EST. June readings with 1 percent synchronization between A and B sensors averaged 14 percent higher than those taken with 5 and 10 percent synchronizations; however, levels of synchronization did not affect readings taken in March and December.

For both the May and August data, a log-log regression model was found to be most suitable for calibrating visual estimates of LAI. In this model, the interaction of visually estimated LAI and stand basal area explained 55 to 68 percent of the variation in LAI-2000 estimates. Average height explained an additional 8 to 18 percent of variation. None of the indicator variables for individual observers were significant in the model, indicating an absence of bias.

CONCLUSIONS

Results of this research indicate that the LAI-2000 is a relatively accurate and precise instrument for estimating LAI of loblolly pine plantations. The instrument overestimated LAI slightly when compared to needlefall estimates. No significant drift was found in repeat measurements taken in rapid succession. On the average, the LAI-2000 gave somewhat higher readings under cloudy versus clear sky conditions. Readings were higher when taken during mid-morning versus late morning or early afternoon. Apparently bright sky conditions cause slight reductions in LAI-2000 estimates. Of all accuracy and precision tests, levels of synchronization between A and B sensors resulted in the greatest variation among readings. When synchronization between the two sensors was low (5 or 10 percent differences) during the June readings, LAI-2000 estimates were reduced in value relative to the 1-percent synchronization; however, this trend was not observed in the March and December readings. Thus, a high degree of synchronization (1-percent difference) is critical if the sensor is to detect change in LAI during the growing season.

The interaction of visually estimated LAI and stand basal area was the best single variable for predicting May or August LAI-2000 readings. This result suggests that visual estimates of LAI are influenced by stand basal area. In support of this finding, Sampson and others (1996) recommend a linear adjustment to visually estimated LAI to account for deviations in basal area from what would be considered full stocking. Average height, an indicator of age and site productivity, also was a significant variable in the regression models. The visual estimates of LAI were not influenced by potential bias from individual observers.

Our research has indicated that visual estimates of LAI can be successfully calibrated with more objective estimates obtained using needlefall collections or optical sensors. This combination of techniques can be used to provide a reliable and low cost method for estimating LAI of pine plantations.

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SEASONAL DYNAMICS IN LEAF AREA INDEX IN INTENSIVELY MANAGED LOBLOLLY PINE

Timothy B. Harrington, Jason A. Gatch, and Bruce E. Borders¹

Abstract—Leaf area index (LAI; leaf area per ground area) was measured monthly or bi-monthly for two years (March 1999 to February 2001) with the LAI-2000 in intensively managed plantations of loblolly pine (*Pinus taeda* L.) at Eatonton and Waycross GA. Since establishment of the three age classes at each site, the stands have received combinations of complete weed control and annual fertilization. The youngest age class at Eatonton continued to accumulate LAI for the duration of the study, while LAI did not differ significantly among age classes at Waycross. Fertilization caused increases in LAI by as much as a full unit, except in the youngest age class at Eatonton. Seasonal development of LAI from associated hardwoods and shrubs was more evident for the deciduous community at Eatonton than for the evergreen community at Waycross. The LAI-2000 successfully detected differences in LAI due to seasonal change, stages of stand development, stand nutrition, and presence or absence of non-pine woody vegetation.

INTRODUCTION

Leaf area is the most important morphological feature affecting productivity of a forest stand because it is the primary site of energy and gas exchange for photosynthesis and respiration. Soon after crown closure, forest stands begin an asymptotic approach to their maximum LAI. Maximum LAI occurs at full stocking and it can vary with site quality and silvicultural inputs. Recent interest in the use of LAI as a management diagnostic for predicting stand productivity and potential for treatment response of loblolly pine has prompted the development of field estimation techniques (Sampson and others 1996). However, an incomplete understanding currently exists regarding how LAI varies seasonally, especially for stands managed with different silvicultural intensities. Previous research on LAI of loblolly pine has focused on peak growing season values derived from needlefall or branch samples (Vose and Allen 1988, Dalla-Tea and Jokela 1991, McCrady and Jokela 1996) and has not considered seasonal dynamics. Therefore, the objective of this research was to characterize seasonal dynamics of loblolly pine LAI as influenced by weed control and fertilization.

METHODS

The research was conducted at mechanically prepared sites in the Piedmont (Eatonton) and Lower Coastal Plain (Waycross) of Georgia. Four treatments were compared: 1) untreated check, 2) annual fertilization with nitrogen, plus first- and second-year applications of phosphorus and potassium, 3) complete weed control, and 4) the combination of annual fertilization and complete weed control. At each site loblolly pine was planted at a 2.4-meter square spacing in 0.15-hectare plots. Each treatment was replicated in two blocks per site. To study treatment effects over different time periods, the entire study was planted at each

site during different years to provide three age classes: oldest (1987 and 1988 plantings for Waycross and Eatonton, respectively), middle (1989 and 1990 plantings) and youngest (1993 and 1995).

Monthly or bimonthly measurements of LAI were taken from March 1999 to February 2001 with the LAI-2000 canopy analyzer (Li-Cor, Inc., Lincoln NB). A total of twelve LAI readings were taken at the same randomly located points on each plot. An above-canopy sensor logged readings in a nearby large opening (no vegetation at greater than 15 degrees above the horizon) while a below-canopy sensor was used to log readings within the study area. All LAI-2000 readings were taken with the sensor facing north at 1.4 meters above ground and a 90-degree view cap attached to the lens. In the laboratory, data from the two sensors were merged and LAI was calculated with Li-Cor software. Data from each location were analyzed separately. Plot averages for each sample date were subjected to analysis of variance to test main effects (treatment and age class) and their interaction.

RESULTS

At Eatonton, LAI of the youngest age class continued to increase for the duration of the study, while LAI of the middle and oldest age classes had similar peak values during the 1999 and 2000 growing seasons. The interaction of weed control and age class was significant for most of the sample dates. In the youngest age class, LAI was greater in the presence versus absence of weed control because this treatment greatly accelerated the development and dominance of a pine canopy. Shrub and hardwood species contributed little to LAI in these five- to six-year-old stands.

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However, in the oldest age class, growing season LAI was greater in the absence versus presence of weed control because the addition of non-pine woody vegetation increased LAI by up to 30 percent. Fertilization was associated with significant increases in LAI by as much as a full unit, but these responses were limited primarily to the middle and oldest age classes.

At Waycross, there were no significant differences in LAI among age classes. In addition, the effects of weed control and fertilization were additive and did not interact significantly with age class. Weed control was associated with a reduction in LAI because of the resulting absence of non-pine woody vegetation. Fertilization was associated with increases in LAI by as much as a full unit.

At each site, increases in LAI from fertilization were sustained throughout the growing and dormant seasons. This indicates that the pine canopy is maintaining a larger surface area of needles throughout the year, and not just during periods of active shoot growth.

Development of LAI in the absence of weed control differed strongly between the two sites. At Eatonton, LAI of the deciduous hardwood and shrub community climbed rapidly in the spring and declined rapidly in the fall. At Waycross, the seasonal change in LAI resulting from associated hardwoods and shrubs was less conspicuous, probably because many of the species are evergreen, such as gallberry (*Ilex glabra* L.) and wax myrtle (*Myrica cerifera* L.).

CONCLUSIONS

LAI development of the youngest age class at Eatonton lagged behind that of Waycross. Likewise, LAI responses to fertilization were not yet detectable in the youngest age class at Eatonton. In contrast, peak LAI values and responses to fertilization and weed control differed little

among age classes at Waycross. Thus, stands of the youngest age class at Eatonton continued to accumulate leaf area, while those at Waycross had already reached stable values. Differences in LAI due to stand nutrition were maintained throughout the year, and not just during periods of active shoot growth.

The LAI-2000 was able to detect differences in LAI of loblolly pine plantations attributable to seasonal change, age class, stand nutrition, and presence or absence of non-pine woody vegetation. Subtle differences in seasonal rates of LAI development between deciduous and evergreen hardwood and shrub communities also were evident.

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COMPARISON OF GROWTH EFFICIENCY OF MATURE LONGLEAF AND SLASH PINE TREES

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Abstract—Variation in aboveground biomass partitioning (between the stem, branches, and foliage) of mature trees is a key determinant of growth potential. Investment of photosynthate in crown components generally results in greater overall biomass production of longer duration. The increased production of crown components may be an investment in longterm aboveground production and can result in increased growth efficiency (defined as biomass increment per unit leaf area). This study was initiated to compare the relationships of crown structure to aboveground allocation and stemwood growth for mature planted slash pine (*Pinus elliottii* Engelm.) and naturally regenerated longleaf pine (*P. palustris* Mill.) trees. Total tree height, diameter at breast height, height to base of the live crown, and bark thickness were measured and increment cores taken from longleaf and slash pine trees of similar ages growing on similar sites. These data were used with allometric equations, developed previously for each species from destructive sampling procedures at these sites, to predict projected leaf area and 5-year stem biomass production. Growth efficiency for trees was calculated as 5-year stemwood biomass increment per unit projected leaf area. Average (per tree) stem biomass production was not statistically different between longleaf pine and slash pine, nor were average projected leaf areas. Average growth efficiency of longleaf pine was significantly greater than that of slash pine ($P < 0.10$); graphical examination of individual tree data, however, did not indicate strong or significant differences in growth efficiency between species when comparing trees of equal size. These findings suggest that greater investment in crown structural components by longleaf pine may, at the stand-level, help to maintain stemwood production over a longer lifespan relative to slash pine, but individual tree results are less clear.

INTRODUCTION

Crown structure, characterized by the size (biomass or surface area) and distribution of individual crown elements (i.e., branches, shoots, and foliage), is a key variable in forest ecological studies. Crown structure is functionally related to tree growth through its inherent relation to radiation interception and gas exchange (Jarvis and Leverenz 1983, Stenberg and others 1994, Teskey and others 1994). It also strongly affects sub-canopy plant diversity by modifying light quantity and quality, thereby affecting understory species composition (Kimmins 1997).

Biomass and surface area equations have been used to determine dry weight allocation patterns, which in turn have been related to productivity. Research has shown that dry matter allocation to foliage, branches, and stemwood is variable and affected by several factors including tree age, species, and climatic conditions (Gholz and Cropper 1991, Gower and others 1994, Teskey and others 1994). Many, and perhaps most, of these studies, however, have investigated the effects of these factors on dry weight partitioning in young trees, with far fewer studies looking at allocation patterns in mature trees. For example, little is known about how mature trees allocate carbon or how the

relationship between crown structure and stemwood growth varies with age for different tree species.

One species comparison of interest is that between longleaf pine (*Pinus palustris* Mill.) and slash pine (*P. elliottii* Engelm.) because of the large overlap in their habitat distributions and because they are often found growing on the same sites. It is generally accepted that slash pine grows more quickly (and probably with greater efficiency) at young ages, but longleaf pine produces more cumulative growth at older ages and over longer time periods (Boyer 1990, Lohrey and Kossuth 1990); i.e., growth rates decline in slash pine at ages greater than 25-30 years whereas longleaf pine growth rates are maintained or may increase for many more years. This presumption has not been rigorously tested for older trees, however, largely due to the lack of older slash pine stands and few comparable stands of longleaf and slash pine growing on similar soils. An additional factor is that slash pine is shorter-lived, generally not exceeding 100-200 years in age (Hebb and Clewell 1976), whereas longleaf pine can live to be as old as 500 years (Landers and others 1995). Thus, the same chronological ages may represent different physiological ages for the two species.

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Table 1—Average stand structural characteristics for the sampled longleaf and slash pine stands

	Longleaf pine	Slash pine
Density (trees/ha)	135	107
DBH (cm)	37.4	41.7
Height (m)	24.1	27.2
Basal area (m ² /ha)	13.3	14.8

In an earlier, unpublished biomass comparison study of longleaf pine and slash pine, we developed allometric equations for predicting stem biomass production and projected leaf area for both species at these sites. That study indicated that mature (60-75 year old) planted slash pine and naturally regenerated longleaf pine exhibited strong differences in aboveground allocation between foliage, branches, and stemwood. The objective of this study was to use the allometric equations developed in the previous study in conjunction with recent growth measurements to examine how patterns of allocation affect growth efficiency in mature longleaf pine and slash pine stands growing on similar sites.

METHODS

Site Descriptions

This study was conducted at the Joseph W. Jones Ecological Research Center located in Baker County, Georgia (31° 13'N, 84° 29'W). Two specific sites were sampled: a 52 hectare stand dominated by naturally regenerated longleaf pine (average age of 73 years), and a 77 hectare slash pine stand planted in 1938. Both sites are located on well-drained upland and fluvial terraces, and the soils are Typic and Arenic Hapludults, with loamy sands over sandy loams to sandy clay loams. The soil moisture regime is similar at the two sites. The slash pine stand was thinned periodically and is relatively open, although a small component of younger, naturally occurring slash pine and *Quercus* species occupies the under- and mid-stories. The longleaf pine stand has also had some harvest entries, though less frequently than the slash pine, and contains multiple age classes of longleaf pine. The understory of the longleaf pine stand is dominated by grasses with some hardwoods maintained in a shrubby state through the use of frequent prescribed fire. Stand structural characteristics are summarized in table 1.

Biomass Sampling

Longleaf pine biomass was sampled in 1996 through the destructive sampling of 23 trees representing the range of tree diameters in the stand. Common biomass sampling techniques were employed, including the measurement of stem diameter and collection of disks at fixed points along the stem, measurement of all branch diameters and lengths, measurement of total green weight of the stem, branches and foliage in the field, and the collection of

subsamples from each component to determine fresh weight:dry weight ratios. In addition, projected leaf area per unit dry weight of foliage was determined in the laboratory. Sixteen slash pine trees were sampled in 1998 using comparable field and laboratory methodologies. These data were used to develop allometric prediction equations for each species to predict individual tree stem, branch and foliage biomass and projected leaf area from easily measured parameters.

Growth Measurements and Calculations

Six 0.5 hectare plots were established for sampling biomass increment and growth efficiency, with 3 plots in each stand type (longleaf and slash pine). At each plot all trees greater than 15 centimeter dbh were sampled for a total of approximately 50-65 trees per plot. Total tree height, diameter at breast height, height to the base of the live crown, and bark thickness were measured. In addition, two increment cores were extracted at right angles from every tree and measured for 5-year radial increment.

Using these data and the previously developed allometric equations, aboveground biomass allocation and projected leaf area were predicted for each tree, and a 5-year stem biomass increment calculated using the radial increment measurements. Growth efficiency was calculated for each tree as the 5-year stem biomass increment divided by the projected leaf area.

Statistical Analyses

T-tests were conducted to determine if differences in stem biomass production, projected leaf area and overall growth efficiency existed between species, with statistical significance set at $\alpha = 0.10$. Also, linear regressions were developed for the transformed individual tree data and the slopes of the relationships compared for the two species.

RESULTS

The average aboveground biomass allocation, as predicted from the allometric equations, differed considerably between species as shown in figure 1. Longleaf pine had more than double the percentage allocation to crown components in comparison to slash pine, and this same doubling effect also held true for the individual crown components (branches and foliage). In other words, for equal size trees, slash pine allocated significantly more biomass increment to the stem than did longleaf pine.

Table 2—Comparison of average per tree values calculated for projected leaf area, stem biomass increment and stem growth efficiency for longleaf and slash pine. Statistical comparisons were conducted using T-tests

	Longleaf Pine	Slash Pine	P>T
Projected leaf area (m ²)	100.5	93.2	0.14
Stem biomass increment(kg)	53.4	52.7	0.78
Growth efficiency (kg/m ²)	0.64	0.58	0.07

When comparing average tree-level values (table 2) we found that projected leaf area and 5-year stem biomass increment did not differ statistically between species. Average growth efficiency was significantly greater for longleaf pine (table 2), indicating that, on average, longleaf pine produced more stem biomass per unit of projected leaf area than slash pine. Yet when the individual tree data for stem increment and growth efficiency were plotted versus projected leaf area (figure 2), no clear species differences were apparent. Linear regressions of log-transformed data for growth efficiency as a function of projected leaf area produced significantly different slopes (results not shown). Given the relationship shown in figure 2, however, we did not think this result was biologically significant but instead was likely only the result of examining dissimilar ranges of data for the two species. Figure 3 indicates that the species do segregate based upon stand-influenced structural characteristics, as indicated by the index of modified crown ratio (defined as live crown length divided by (height - 1.3 meters)).

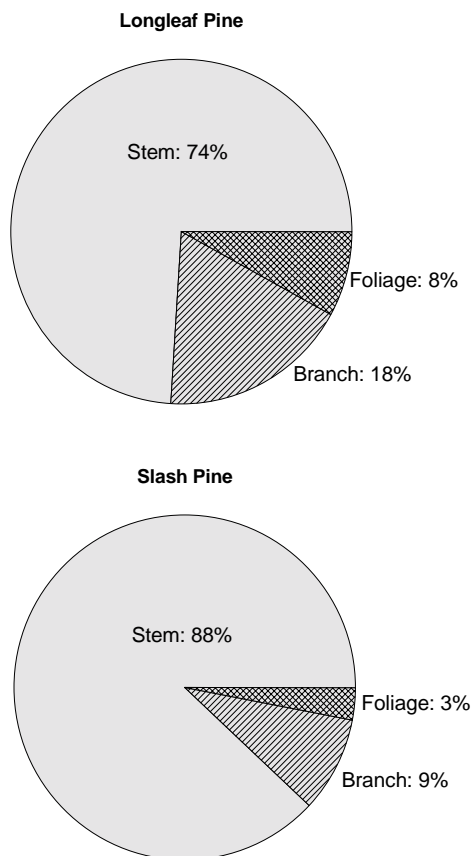


Figure 1—Average aboveground biomass distribution (by percent) for longleaf pine (top) and slash pine (bottom).

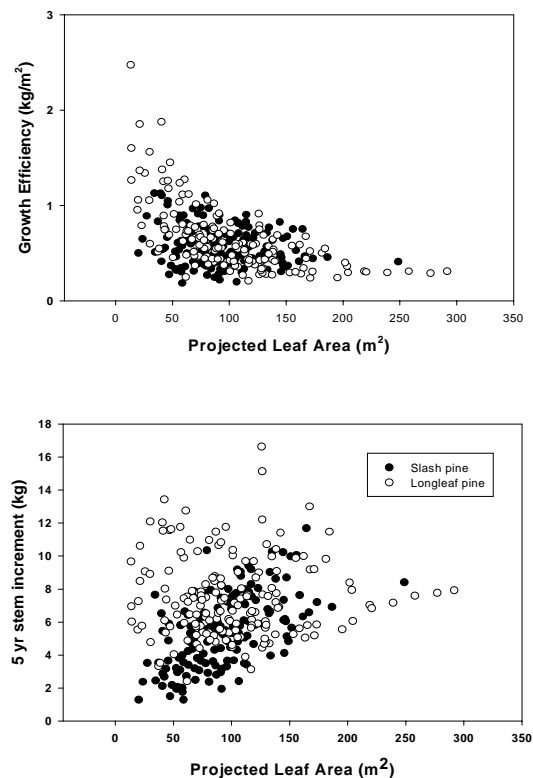


Figure 2—Relationship between 5-year stem biomass increment (top) and stem growth efficiency (bottom) and projected leaf area for all sampled trees.

DISCUSSION

Studies of resource allocation in other species suggest that stemwood accumulation relative to branches and foliage increases with age, stand density and site quality (Binkley 1983, Espinosa Bancalari and Perry 1987, Fogel and Hunt 1983, Keyes and Grier 1981, Turner and Long 1975). Younger or more open stands, or stands growing on poor sites, tend to have a relatively higher proportion of biomass in foliage and branches (e.g., Binkley 1983), whereas older or denser stands invest relatively less in crowns (e.g., Espinosa Bancalari and Perry 1987 for density).

It is clear from figure 1 that the two species, though of similar age and growing on comparable sites, allocate aboveground growth quite differently. This result was not surprising given the known differences in growth patterns and the visually distinct crown forms of the two species. What was surprising, however, is that these different patterns of allocation did not lead to significant differences in per tree projected leaf area or stem biomass increment for the 5-year period measured.

The lack of clear differences in stem increment between species was contrary to the results we expected given the ages of the trees in this study. Plantation grown 60-year-old slash pine are likely at a more advanced physiological age

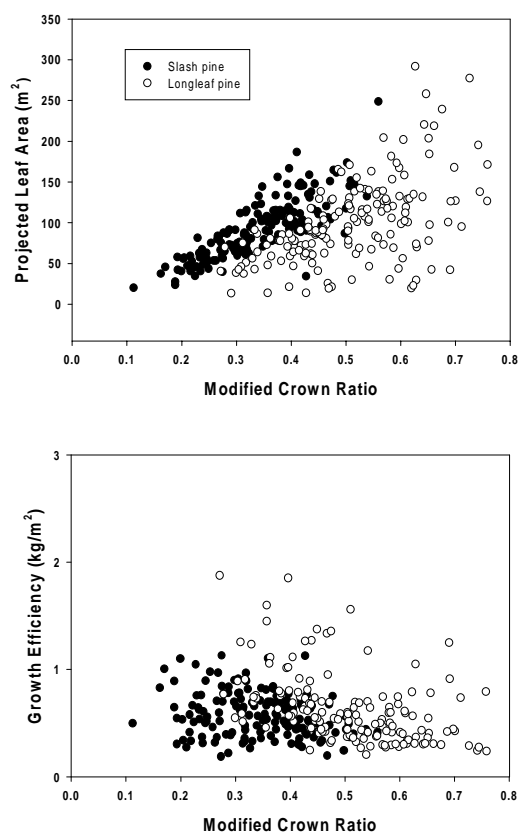


Figure 3—Influence of stand and tree structure, as indicated by a modified crown ratio (live crown length divided by (total tree height - 1.3)), on per tree projected leaf area (top) and stem growth efficiency (bottom).

than 73-year-old (on average) longleaf pine in a natural stand. We therefore expected that production in slash pine would have declined and the longleaf pine would, on average, have higher production. Past stand management must be taken into account, however. The slash pine stand was thinned for a research study subsequent to the biomass sampling but prior to the plot sampling for growth predictions. Thus, the slash pine results presented here are from the residual trees (not marked for removal) and represent the best growing individuals in the stand, as was documented in a companion study from the same area (McConville and others 1999). In this instance, then, we actually compared the “best” slash pine trees with randomly selected trees from the longleaf pine stand (i.e., not those selected for good growth). This fact could have an effect on the results presented.

The results for growth efficiency were also not quite as we expected a priori. Growth efficiency was higher on average for longleaf pine (table 2). But, upon examining results for individual trees (figure 2), any differences in the average values appear to be due to disparities in the range of data included in the sample rather than to true biological differences between the species. The form of the

relationship between growth efficiency and leaf area found in figure 2 is typical of those found for other shade intolerant species where light is not a limiting factor (Roberts and others 1993). The negative exponential form of the relationship can be attributed to variation in structural characteristics of the canopy (Roberts and others 1993); figs. 1 and 3 indicate that there are some differences in canopy structure for the two species, and these differences may in part explain the observed small differences in growth efficiency between slash and longleaf pine.

The discussion so far has focused on results for individual trees. When comparing stem growth at the stand-level, however, the relatively small differences measured for individual trees may become more significant. That is, the longleaf pine stand had higher tree densities (table 1); thus, if these trees had the same or slightly higher average stem increment or growth efficiency, then the total, stand-level production of longleaf pine will be greater than for slash pine. It is important not to push this line of reasoning too far, however, because the results represent only a single case study.

CONCLUSIONS

Despite expectations, in this study the stem biomass increment and projected leaf area of mature longleaf and slash pine did not differ significantly even though there are clear differences in the allocation of aboveground biomass. Also, the statistical differences in average growth efficiency were not apparent when data from all individual trees were examined. The lack of clear differentiation between species is probably attributable to past stand history and management, but this factor should be investigated more closely through additional studies.

In short, individual trees of the two species with similar chronological ages and grown on comparable sites do not appear to produce greatly different stem biomass for a given tree size. There may, however, be some disparities in stand-level production, at least as indicated by the results of this one study. For longterm planning purposes an additional consideration is the known difference in longevity for the two species, which could affect how long each species can be expected to maintain adequate stand stocking over long rotations.

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PHOTOSYNTHETIC LIGHT RESPONSE OF BOTTOMLAND OAK SEEDLINGS RAISED UNDER PARTIAL SUNLIGHT

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Abstract—Seedlings of cherrybark oak (*Quercus pagoda* Rafinesque), Nuttall oak (*Quercus nuttallii* Palmer) and overcup oak (*Quercus lyrata* Walter) were grown under two light levels, partial (20 percent) or full sunlight, to study physiological acclimation of leaves to low light availability. Shifts in leaf morphology were noted for seedlings raised beneath partial sunlight, and photosynthetic light response curves indicated that bottomland oaks varied in their degree of physiological acclimation to low light availability. Greatest shifts in leaf function under partial sunlight were observed for cherrybark oak which exhibited a 48 percent decrease in net photosynthesis at light saturation (P_{n-sat}), and a 55 percent decrease in dark respiration rate (R_d) (based on leaf area). These adjustments to the photosynthetic mechanism were accompanied by a 46 percent decrease in the light compensation point (LCP). In contrast, Nuttall oak leaves showed similar rates of P_{n-sat} , R_d and apparent quantum yield (ϕ) regardless of the light environment in which they developed. Overcup oak leaves were intermediate in response exhibiting a 53 percent decreased in R_d and a 57 percent increase in ϕ , but P_{n-sat} was not decreased for leaves grown under partial sunlight. Silvicultural implications of these results for bottomland oak regeneration are presented.

INTRODUCTION

Bottomland hardwood forests of the southern United States characteristically support a rich diversity of tree species. Of the more than 70 tree species endemic to major and minor river bottoms, bottomland oaks are often primary components of many species-site associations (Putnam and others 1960). Though bottomland oaks are often a primary component of mixed species, bottomland hardwood stands, regeneration of these desired species can be problematic. The problem of obtaining an adequate stocking of vigorous oak (*Quercus* spp.) reproduction following regeneration harvests in southern bottomlands has been addressed by numerous authors for several decades (Chambers and others 1987, Hodges and Janzen 1987, Johnson 1975, Nix and others 1985). Yet, reliable techniques for securing oak regeneration in bottomlands are still unavailable. A stronger understanding of how environmental factors regulate oak seedling establishment and growth is clearly needed to develop silvicultural practices that foster oak regeneration (Hodges and Gardiner 1993).

Previous research in bottomlands has identified several environmental factors that potentially contribute to oak regeneration problems. For example, flooding is a prominent factor in bottomlands that can limit establishment or destroy entire cohorts of oak reproduction (Johnson and Deen 1993, Young and others 1995). Competition from other tree or vine species can be severe in bottomlands, particularly on well drained, productive sites (Gardiner and Yeiser 1999, Johnson 1975). Mast depredation may limit seed tree fecundity, and herbivory often reduces vigor of established seedlings (Johnson 1981, Lockhart and others 2000).

Though many factors potentially contribute to poorly stocked oak regeneration pools in bottomlands, some problems are likely linked to light availability. This may be realized through the observations that oak seedlings are generally intolerant of shade, and light availability in the understory of mature bottomland hardwood forests is generally low (Hodges and Gardiner 1993, Jenkins and Chambers 1989). Recent research has established the importance of sufficient light availability to development of vigorous cherrybark oak (*Quercus pagoda* Rafinesque) reproduction (Gardiner and Hodges 1998). And, silvicultural practices which increase understory light availability can be applied to improve size and vigor of cherrybark oak reproduction (Lockhart and others 2000). Though these findings are promising, much remains to be learned about the basic functioning of oak seedlings relative to their light environment. This experiment was initiated to study the effects of light availability on the photosynthetic light response of seedlings of three bottomland oak species. Additionally, leaf morphology was examined to describe potential changes in functional processes relative to structural acclimation.

METHODS

The experiment was conducted during the 1993 growing season at the Mississippi State University, Blackjack Research Farm located near Starkville, MS (33° 26' N Latitude, 88° 46' W Longitude). Twenty-four, 1-year-old dormant seedlings of cherrybark oak, Nuttall oak (*Quercus nuttallii* Palmer) and overcup oak (*Quercus lyrata* Walter) (72 total seedlings) were transplanted into 18.9-liter pots filled with potting soil and sand (50:50, volume:volume). Pots were fertilized with a 14-14-14 (nitrogen-phosphorous-potassium) time release, granule (Osmocote,

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Grace-Sierra Horticultural Products company, Milpitas, CA), and watered as needed to maintain ample soil moisture. Half of the seedlings were randomly selected and placed in a shade house (20 percent of full sunlight), while the other half were grown under full sunlight in an adjacent field.

Measurements of leaf morphology and physiology began in July after maturation of the second flush of shoot growth. Leaf morphology was characterized through measurements of blade area and leaf mass per area. Measurements were collected on 30 randomly selected leaves for each species and light environment (5 randomly selected leaves from 6 randomly selected seedlings). Blade area (centimeter²) was measured with a digital image analysis system (Decagon Devices Inc, Pullman, WA, USA). Leaves were oven-dried for 48 hours at 70° Celsius, then leaf mass per area was calculated as blade mass ÷ blade area (milligrams centimeter⁻²).

Leaf physiology was characterized by measuring the photosynthetic light response of four randomly selected seedlings for each species and light environment. Seedlings were brought into the laboratory where measurements were conducted on a single, fully developed leaf from the terminal flush. Net photosynthesis (P_n) (micro-moles centimeter⁻² second⁻¹) of each sample leaf was recorded at 6 levels of photosynthetic photon flux density (PPFD) (0, 25, 100, 400, 800, 1600 micromoles meter⁻² second⁻¹) with a LCA-3 gas analyzer and Parkinson leaf cuvette (The Analytical Development Company Ltd, England). P_n measurements on each sample leaf began at the lowest light level and ended with the highest light level. Particular light levels were produced by filtering light from a 300 watt quartz filament bulb with various configurations of neutral density filters. Because of high variation in P_n observed for overcup oak leaves, two additional seedlings from each light environment were sampled for this species.

Curves were fit to photosynthetic light response data according to methods described in Givnish (1988). The model used for this procedure is defined in Equation 1.

$$P_n = [(P_{g-sat} \times PPFD) \div (K + PPFD)] - R_d \quad (1)$$

For Equation 1, P_n is net photosynthesis, P_{g-sat} is gross photosynthesis at leaf saturation, PPFD is photosynthetic photon flux density, K is the PPFD required to achieve half of P_{g-sat} , and R_d is the dark respiration rate. The light compensation point (LCP) for each leaf was calculated with Equation 2.

$$LCP = (-K \times R_d) \div (R_d - P_{g-sat}) \quad (2)$$

Apparent quantum yield (ϕ) of each leaf was calculated with the first derivative of Equation 1 with PPFD set at LCP as presented in Equation 3.

$$\phi = P_{g-sat} \times K \div (K^2 + 2K \times PPFD + PPFD^2) \quad (3)$$

The effect of light availability on photosynthetic light response variables (P_{n-sat} , LCP, R_d , K) and leaf morphology variables (blade area, leaf mass per area) were analyzed with analysis of variance procedures according to a completely random design for each species. All tests were conducted at an α of 0.05.

RESULTS AND DISCUSSION

Leaf Morphology

Leaves of all three oak species examined in this study exhibited morphological acclimation when seedlings were raised under 20 percent sunlight. Cherrybark oak showed the greatest blade area response with a 129 percent increase on leaves that developed under partial sunlight (table 1). Blade area of Nuttall oak increased 103 percent, while blade area of overcup oak showed a 67 percent increase. Observations on blade area increases from this study illustrate the magnitude of variation in morphological acclimation expressed by different North American oak species. Others have reported blade area increases of 110 percent for bur oak (*Quercus macrocarpa* Michaux), 108 percent for chinkapin oak (*Quercus muehlenbergii* Engelman), and 208 percent for coast live oak (*Quercus agrifolia* Nee) when these species developed under partial sunlight (Callaway 1992, Hamerlynck and Knapp 1994).

Table 1—Morphological characteristics (mean ± standard error)^a of leaves from three bottomland oak species raised under full (100 percent) or partial (20 percent) sunlight

Light Level	Cherrybark Oak	Nuttall Oak	Overcup oak
----- Blade Area (cm ²) -----			
Full Sunlight (100 pct)	35.7 ± 1.8 b	25.6 ± 1.4 b	25.2 ± 1.2 b
Partial Sunlight (20 pct)	81.9 ± 4.8 a	52.1 ± 2.4 a	42.1 ± 2.5 a
----- Leaf Mass per Area (mg cm ⁻²) -----			
Full Sunlight (100 pct)	11.9 ± 0.2 a	11.0 ± 0.2 a	9.8 ± 0.2 a
Partial Sunlight (20 pct)	7.0 ± 0.2 b	6.8 ± 0.1 b	6.3 ± 0.1 b

^a Means in a column followed by the same letter are not different at $\alpha = 0.05$.

Table 2--Photosynthetic light response variables (mean \pm standard error)^a for three bottomland oak species raised under full (100 percent) or partial (20 percent) sunlight

Light Level	Cherrybark Oak	Nuttall Oak	Overcup oak
----- Net Photosynthesis Rate (mol m ⁻² s ⁻¹) -----			
Full Sunlight (100 pct)	12.9 \pm 1.0 a	10.7 \pm 0.7 a	10.5 \pm 1.5 a
Partial Sunlight (20 pct)	6.8 \pm 0.9 b	9.6 \pm 1.2 a	7.5 \pm 1.4 a
----- Light Compensation Point (mol m ⁻² s ⁻¹) -----			
Full Sunlight (100 pct)	18.3 \pm 1.6 a	18.2 \pm 3.4 a	22.9 \pm 2.1 a
Partial Sunlight (20 pct)	9.8 \pm 2.3 b	11.3 \pm 0.7 a	7.1 \pm 1.1 b
----- Dark Respiration Rate (mol m ⁻² s ⁻¹) -----			
Full Sunlight (100 pct)	0.9 \pm 0.06 a	0.8 \pm 0.14 a	0.9 \pm 0.16 a
Partial Sunlight (20 pct)	0.4 \pm 0.15 b	0.6 \pm 0.16 a	0.4 \pm 0.08 b
----- Apparent Quantum Yield -----			
Full Sunlight (100 pct)	0.05 \pm 0.006 a	0.04 \pm 0.003 a	0.04 \pm 0.006 b
Partial Sunlight (20 pct)	0.04 \pm 0.005 a	0.05 \pm 0.011 a	0.06 \pm 0.004 a
----- Saturation Constant (mol m ⁻² s ⁻¹) -----			
Full Sunlight (100 pct)	319 \pm 57 a	279 \pm 53 a	319 \pm 12 a
Partial Sunlight (20 pct)	226 \pm 75 a	235 \pm 35 a	142 \pm 38b

^a Means in a column followed by the same letter are not different at $\alpha = 0.05$.

Coupled with the increase in blade area, all species showed a reduced leaf mass per area when raised beneath partial sunlight (table 1). These reductions in mass per area ranged from 41 percent for cherrybark oak to 36 percent for overcup oak. Reductions in leaf mass per area probably result from a decrease in leaf thickness that can be attributed to a decrease in palisade cell stacking, a decrease in leaf cuticle thickness, and/or a decrease in epidermal and palisade cell thicknesses (Ashton and Berlyn 1994, Carpenter and Smith 1981, Jackson 1967). The range of response in mass per area observed between bottomland oaks in this study was comparable to other oak species endemic to the northern United States. Abrams and Kubiske (1990) reported that leaf mass per area decreased under low light availability by 35 percent for northern pin oak (*Quercus ellipsoidalis* E. J. Hill), 36 percent for northern red oak (*Quercus rubra* Linnaeus), 43 percent for bur oak and white oak (*Quercus alba* Linnaeus), and 56 percent for black oak (*Quercus velutina* Lamarck).

For many broadleaved tree species, leaves which developed under low light conditions will usually have enlarged leaf blades and a lower mass per area than those which have developed under ample light availability (Abrams and Kubiske 1990, Jackson 1967, Goulet and Bellefleur 1986). The three bottomland oaks examined in this experiment were no exception. Physiological function of oak seedlings growing in low light environments may benefit from this

morphological acclimation. Leaf physiology of oak seedlings may be improved by several mechanisms including increasing the light gathering area of individual leaf blades, increasing the efficiency of harvesting diffuse sunlight because chloroplasts are closer to the leaf surface, and reducing the respiratory demand of leaves per unit area (Chow and others 1988, Hamerlynck and Knapp 1994, Man and Lieffers 1997, Kozlowski and others 1991).

Leaf Physiology

Photosynthetic light response curves revealed that acclimation of the photosynthetic mechanism to low light availability differed between the three bottomland oak species (figure 1, table 2). Cherrybark oak seedlings which developed beneath partial sunlight showed a 50 percent reduction in P_{n-sat} (table 2). This is in contrast to P_{n-sat} rates observed for Nuttall oak and overcup oak, which did not show a decrease when seedlings were raised under partial sunlight. The reduced photosynthetic capacity observed for cherrybark oak is consistent with another report on this species, and observations on other shade intolerant broadleaved species (Bazzaz and Carlson 1982, Gardiner and Krauss In Press, Kubiske and Pregitzer 1996). It is not known why Nuttall oak and overcup oak behaved differently, but a light environment effect on overcup oak may have been obscured by the high variance associated with P_{n-sat} for this species (figure 1, table 2). Photosynthetic capacities of seedlings receiving full sunlight in this study were

generally higher than reported observations on field-grown cherrybark oak and Nuttall oak seedlings (Gardiner and others In Press, Sung and others 1999).

In addition to decreased P_{n-sat} , cherrybark oak seedlings raised under partial sunlight exhibited a 55 percent decrease in R_d (table 2). R_d of overcup oak was similarly reduced, but R_d for Nuttall oak was not altered by light regime (table 2). A decrease in R_d would be expected to accompany reductions in leaf mass per area as noted earlier for these three oak species, because of the reduced cell volume associated with the lower leaf mass per area (Hamerlynck and Knapp 1994, McMillen and McClendon 1983). Results from other studies on cherrybark oak and Nuttall oak are contradictory to the findings in this study. Gardiner and Krauss (In Press) reported a decrease in leaf mass per area for cherrybark oak grown under partial sunlight, but a concomitant decrease in R_d was not measured on those seedlings. And, Nuttall oak grown beneath an eastern cottonwood (*Populus deltoides* Bartram ex Marshall) canopy showed reduced leaf mass per area with a concomitant decrease in R_d (Gardiner and others In Press). These conflicting results indicate that the relative change in leaf mass per area and other uncontrolled environmental factors probably contributed to the disparate results noted between studies. For example, leaf temperature can have a strong effect on R_d , and this variable likely differed between experiments. In the work published by Gardiner and others (In Press) and Gardiner and Krauss (In Press), leaf cuvette temperature was controlled during R_d measurements. Sampling techniques used in this study were not amenable to controlling cuvette temperature.

Associated to the reduced R_d , LCP decreased 46 percent and 69 percent, respectively, for cherrybark oak and overcup oak leaves raised under partial sunlight (table 2). Though of overcup oak increased when seedlings developed under partial sunlight (figure 1, table 2), light environment did not alter ϕ of cherrybark oak, nor did it impact LCP or ϕ of Nuttall oak. Three other North American oaks exhibited similar reductions in LCPs when leaves were acclimated to low light environments (Kubiske and Pregitzer 1996, Hamerlynck and Knapp 1994). Results from those studies confirm the observation that LCPs were lowered primarily through decreased R_d rather than through an increased ϕ . However, the higher ϕ observed for overcup oak seedlings raised under partial sunlight in this study may have lead to a decreased K , which was not observed for cherrybark oak or Nuttall oak (table 2).

MANAGEMENT IMPLICATIONS

Though this study does not consider whole-plant response to light environment, several implications for management of bottomland oak regeneration may be inferred from leaf-level response patterns. First, stand structure of many mixed hardwood forests restricts availability of sufficient light to maximize seedling carbon assimilation. The three bottomland oaks studied appear to require more than 25 to 30 percent of available sunlight for light saturation requirements. Light availability in the understory of mixed bottomland hardwood stands is typically less than 10 percent of available sunlight (Jenkins and Chambers 1989, Lockhart

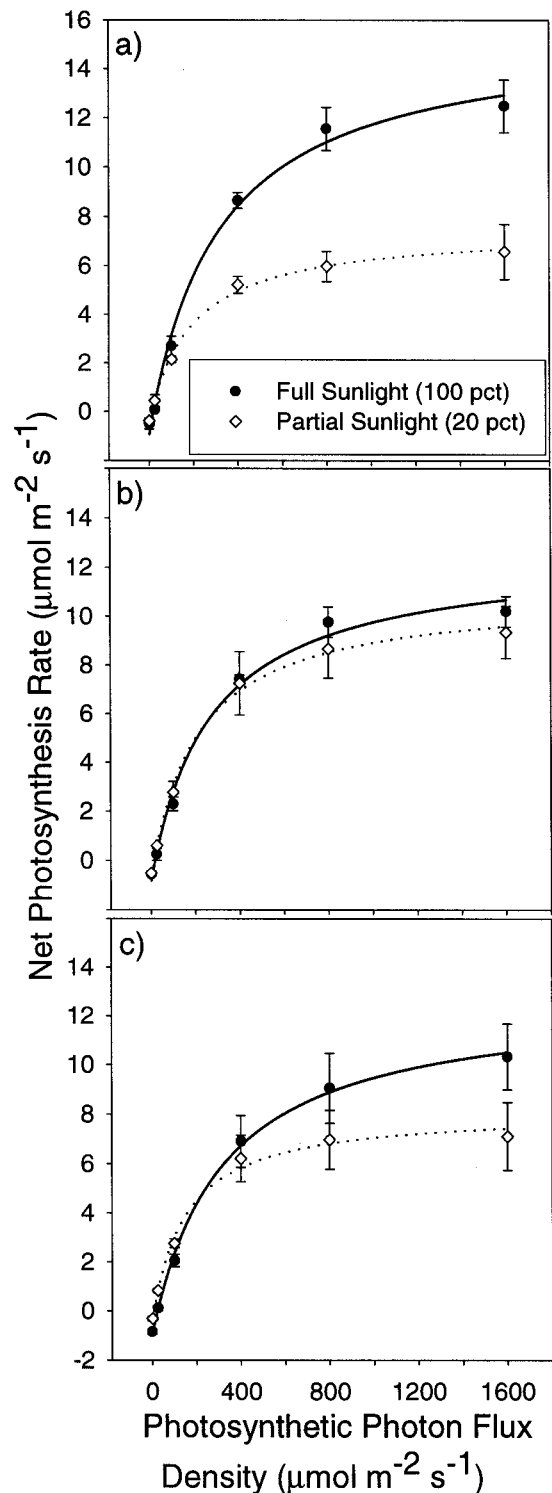


Figure 1—Photosynthetic light response of cherrybark oak (a), Nuttall oak (b) and overcup oak (c) seedlings raised under full (100 percent) or partial sunlight (20 percent).

and others 2000). This study provides physiological evidence supporting the argument that managers will have to implement practices that provide stand structures which improve understory light availability to promote establishment and growth of bottomland oak reproduction (Lockhart and others 2000).

Secondly, bottomland oak seedlings appear to have different light requirements. For example, establishment and growth of cherrybark oak seedlings might require a greater level of understory light availability than other species. The complex aspect of this implication is that bottomland oak species are often found on different sites with different species associations. So, a treatment that provides sufficient light for overcup oak in a slough, may not be adequate for facilitating establishment and growth of cherrybark oak on a ridge.

Related to the second implication is that the different light requirements for each species may also directly effect the length of time seedlings can remain in an understory before being released. Species like Nuttall oak or overcup oak may persist in the reproduction pool of the understory longer than a species like cherrybark oak. Indeed, Johnson (1975) noted that Nuttall oak could persist in the understory for 15 years if seedlings received about 2 hours of direct sunlight a day.

A final management implication gathered from this research revolves around the observation that bottomland oaks differed in their degree of acclimation to light availability. The physiological acclimation observed for cherrybark oak was in association with relatively large shifts in leaf morphology. The implication is that oak seedlings, particularly cherrybark oak, will have to develop a new leaf flush to respond to a richer light environment. It is not known if a species like Nuttall oak, which shows relatively little morphological and physiological acclimation to light availability, can respond quicker to release than a species like cherrybark oak. Nevertheless, oak seedlings will probably require acclimation time before responding to release. A similar finding was noted by Gardiner and Hodges (1998) who considered acclimation of cherrybark oak seedling morphology under various light levels. The slow response to release by cherrybark oak may be seen in the research of Lockhart and others (2000) and Janzen and Hodges (1985). In each of these studies, seedlings required about 3 years before significant response was realized. Regeneration strategies will have to account for this delayed response.

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RESPONSES OF TREE CROWN CONDITIONS TO NATURAL AND INDUCED VARIATIONS IN THROUGHFALL

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Abstract—Concentrations of greenhouse gases, such as carbon dioxide, methane, and oxides of nitrogen, in the atmosphere are predicted to double in the next one hundred years. Forecasts of climatic variation across the southeastern United States resulting from these increases range from higher average temperatures and decreased summertime precipitation to lower maximum temperatures and greater precipitation. Since 1993, the effects of increased and decreased precipitation have been studied on an upland hardwood forest in the Walker Branch Watershed near Oak Ridge, TN. Soil moisture was altered by gravity-driven transport of throughfall from a 'dry' (-33 percent of ambient) treatment plot across an ambient treatment plot to a 'wet' (+33 percent of ambient) treatment plot. Beginning in August 1996, crown conditions of saplings and mature trees were monitored annually for responses to seasonal and treatment-related differences in soil moisture. The crown condition classification system developed by the USDA Forest Service, Forest Health Monitoring Program (FHMP) was used to rate tree crowns according to five variables: crown diameter, live crown ratio, foliage density, foliage transparency, and crown dieback. Preliminary analyses indicate differences in crown condition variables between soil moisture treatments and between years within treatments. A full analysis of five years of data, including August 2000, is presented. Results are discussed in relation to climate change predictions for the southeastern United States, and the usefulness of the FHMP crown condition classification system for monitoring forest health in a changing environment.

INTRODUCTION

Researchers have predicted concentrations of atmospheric greenhouse gases, such as carbon dioxide, methane, and oxides of nitrogen, to double in the next one hundred years (Edmonds and others 1984; Freidli and others 1986), thereby increasing the greenhouse effect and leading to an estimated increase in global mean temperature of between 1.5 and 4.5° Celsius (National Academy of Sciences 1983). Uncertainty exists in the predictions of how climate will be altered by the predicted increases in greenhouse gases. Depending on which climate change models are used, forecasts of climatic variation resulting from increases in greenhouse gases range from decreases in summertime precipitation from 5 to 10 percent and increases in wintertime precipitation (Karl and others 1991) to greater summertime precipitation with lower maximum temperatures and higher minimum temperatures (Idso and Balling 1992).

The Throughfall Displacement Experiment (TDE), located on Walker Branch Watershed at the Oak Ridge National Laboratory near Oak Ridge, Tennessee, was designed to study changes in ecological processes that might occur by decreasing hydrologic inputs to one area of a forest while increasing them in an adjacent part of the forest (Hanson and others 1998). Since 1996, indicators of tree crown health have been monitored in response to throughfall

displacement in the canopy of this upland hardwood forest in eastern Tennessee. Measurements of crown responses to either increased or decreased soil moisture resulting from displaced throughfall, were estimated for crown variables using a protocol developed for the Forest Health Monitoring Program (FHMP), State and Private Forestry of the US Forest Service (USDA Forest Service 2001).

This research was designed to utilize the unique hydrological manipulations occurring on the TDE site in an attempt to document any changes in tree crown appearance occurring from decreased or increased soil moisture resulting from the manipulation. This research has as its basis general principles of ecophysiological responses of plants to their environment. For example, a plant growing in soil that begins to dry out will typically allocate more carbon resources to roots at the expense of shoots in an effort to obtain more water. If this effect were to become great enough, tree crowns with reduced mass would appear more transparent, less dense, and perhaps exhibit branch dieback. These crown symptoms are typical of those associated with oak decline, a disease syndrome common in eastern hardwood forests (Ammon and others 1989) and often triggered by drought events (Maass 1989, Myers and Killingsworth 1992, Tainter and others 1990). An objective of this study was to determine the usefulness of the FHMP crown rating protocol in evaluating oaks (*Quercus* spp.) in decline.

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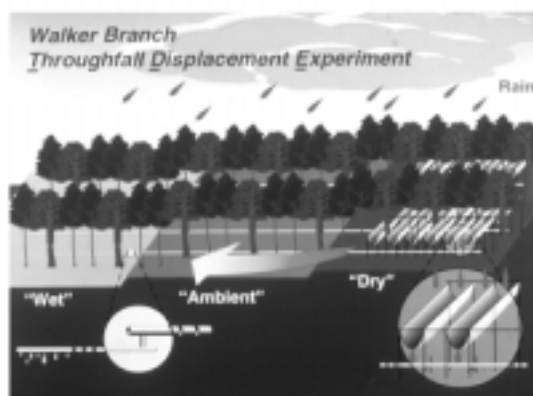


Figure 1—Schematic diagram of the Throughfall Displacement Experiment, Walker Branch Watershed, Oak Ridge National Laboratory, Oak Ridge, TN. Throughfall is captured in plastic troughs beneath the canopy of the Dry plot, flows by gravity through pvc pipes across the Ambient plot, and is released through small holes onto the Wet plot.

METHODS

The site for the Throughfall Displacement Experiment was chosen because of its uniform slope, consistent soils, a reasonably uniform distribution of vegetation, and its position just below the ridge top of the Walker Branch Watershed. The forest on the Walker Branch Watershed is upland hardwood dominated by white (*Quercus alba* L.) and chestnut (*Q. prinus* L.) oaks, sugar maple (*Acer saccharum* Marsh.), and yellow-poplar (*Liriodendron tulipifera*) in the overstory, red maple (*A. rubrum* L.) and blackgum (*Nyssa sylvatica* var. *sylvatica* Marsh.) in the midstory, and flowering dogwood (*Cornus florida* L.) and sourwood (*Oxydendrum arboreum* (L.) DC.) in the understory. There are about 20 tree species on the watershed. Changes in ecological processes resulting from this large-scale manipulation of throughfall will be evaluated in light of the more than 25 years of reference data collected on the Walker Branch Watershed. Complete information about the TDE study is available on the Internet at: www.esd.ornl.gov/programs/WBW/TDEAAAAA.HTM.

Since 1993, one third of the throughfall released by the forest canopy on the TDE has been captured by an array of troughs and is moved from one section of the forested area by way of a gravity-fed system of pvc pipes to another section of forest (figure 1). The area from which one third of throughfall is being removed is the DRY plot, the area receiving the water captured on the DRY plot is the WET plot, and the area in between which receives an unaltered amount of throughfall is the AMBIENT (AMB) plot. Thus, in terms of ambient throughfall, the DRY plot receives 67 percent of ambient throughfall while the WET plot receives 133 percent of ambient throughfall.

Throughfall is intercepted in about 2000 subcanopy troughs (0.3 x 5 meters) suspended above the forest floor on the DRY treatment plot and is then channeled into the pvc pipe system (figure 1). These catchment-pvc pipe systems have been placed at regular intervals from the top of the site to the bottom. Each treatment plot is 80 x 80

meters. Reductions in soil moisture on the DRY plot were expected to be equivalent to the driest growing seasons of the 1980's drought, which resulted in reduced tree growth of some species.

Each 80 x 80 meter plot is further sub-divided into 64 sub-plots with 10 x 10 meter dimensions. Treatment plots are surrounded by a buffer of 10 x 10 m sub-plots. Each tree on the site greater than 10 centimeters was mapped and measured for height and diameter at the beginning of the study and is remeasured on a regular basis. The health of 30 randomly selected trees of various species throughout the understory, midstory, and overstory on each treatment plot was estimated using the FHMP crown condition rating protocol (USDA Forest Service 2001).

The FHMP crown condition rating protocol consists of five variables: diameter, live crown ratio, foliage density, foliage transparency, and dieback. Crown diameter is the average of the widest transect anywhere in the crown and the transect perpendicular to that, measured on the ground in meters. Live crown ratio is the percentage of the length of the live crown compared to total tree height. Foliage density is the percentage of crown branches and leaves that block light coming through a one-dimensional view of the crown taken as a whole. Foliage transparency is the percentage of the amount of skylight visible through the live, normally foliated portion of the crown viewed in the same manner as density. Transparency is the opposite of density. The estimate of crown dieback is a measure of branch mortality as a percentage of the total possible live crown, including dead branches. Dieback begins at the terminal portions of a branch and proceeds toward the trunk or base of the live crown.

Estimates of crown density and transparency were made using a standardized, printed scale that ranges from 5 percent to 95 percent in increments of 5 percent. Each variable except diameter was estimated by two people and averaged for each tree evaluated. The five variables were estimated in mid August from 1996 to 2000. The throughfall manipulation treatment was in effect three years when crown variable measurements were begun. Two-way ANOVAs were performed on the data for treatments by years and years by treatments. Data from the 30 trees sampled on each plot were used in the analysis without regard to tree crown position in the canopy. Percentage

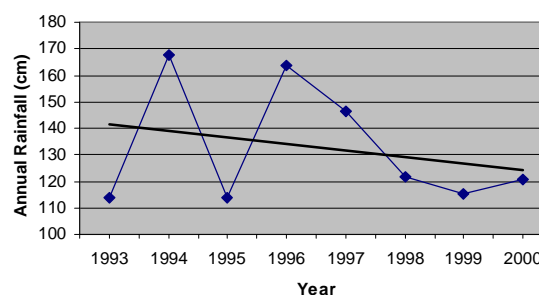


Figure 2—Annual rainfall (with trend line) from 1993 to 2000 at the Throughfall Displacement Experiment site, Walker Branch Watershed, Oak Ridge, TN.

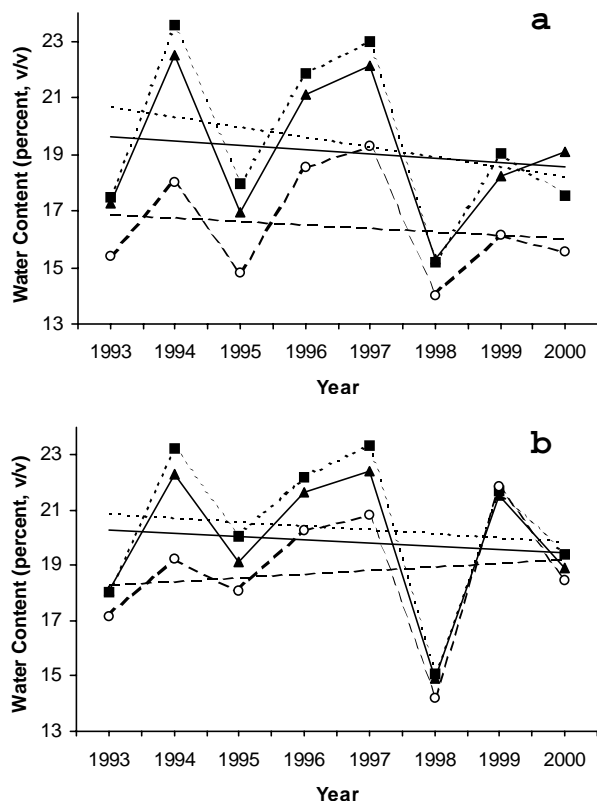


Figure 3— Average soil water contents (percent, v/v) and trend lines for the a) 0 to 35-cm and b) 0 to 70-cm soil profiles on the Wet (■), Ambient (▲), and Dry (○) plots.

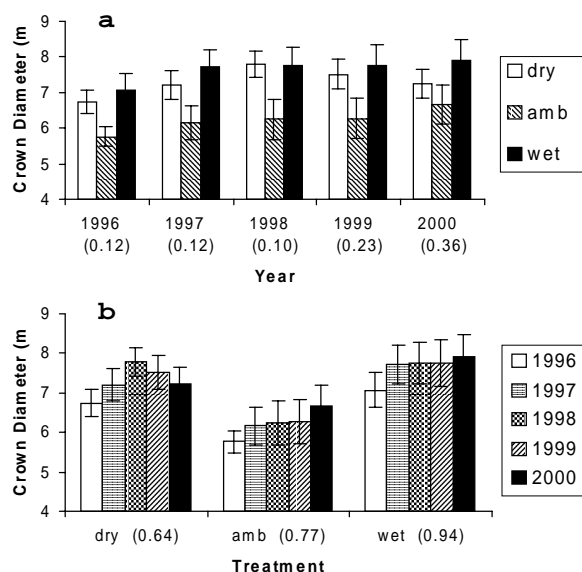


Figure 4—Mean crown diameters (" s.e.m.) of sample trees for a) treatments by years and b) years by treatments. Numbers in parentheses on the x-axis are p-values from the ANOVA tests.

data were transformed using the arcsine function prior to analysis. Tukey's multiple comparisons tests were used to compare variable means.

RESULTS AND DISCUSSION

Rainfall Data

Annual total rainfall at the TDE varied from lows of about 114 centimeters in 1993 and 1995 to a high of about 168 cm in 1994; 1996 had the second highest rainfall (figure 2). Rainfall in five of the eight years was below the trend line of decreasing average precipitation over the treatment period. Starting in 1993, there was a rainfall pattern of low, high, low, and high, followed by a four-year trend of decreasing rainfall.

Soil Moisture Data

This same general increasing and decreasing pattern and overall decreasing trend is evident in soil water content data, as measured by time-domain reflectometry on the three treatment plots, measured in the 0 to 35-cm and 0 to 70-cm layers of soil (figure 3a and b). The effect of throughfall displacement treatments is visible in the soil moisture data from the 0-35 cm layer, with a greater separation evident between the DRY and AMB treatments than between WET and AMB treatments. Treatment separation is less apparent as a function of soil moisture averaged over 70 cm of soil profile.

Crown Diameters

Average annual crown diameters were not affected by throughfall treatments during the five-year measurement period (figure 4a). The average tree crown on the AMB plot tended to be smaller than tree crowns on the DRY and WET plots when first measured in 1996 and they remained that way for the next four years. Crown diameters did not vary from year to year between throughfall treatments (figure 4b).

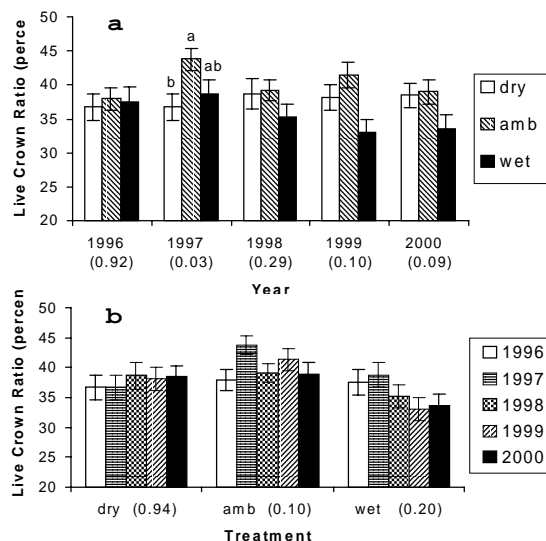


Figure 5—Mean live crown ratios (" s.e.m.) of sample trees for a) treatments by years and b) years by treatments. Numbers in parentheses on the x-axis are p-values from the ANOVA tests. Means with different lowercase letters, in a year or treatment category, differ at $p=0.05$ by Tukey's mean comparison tests.

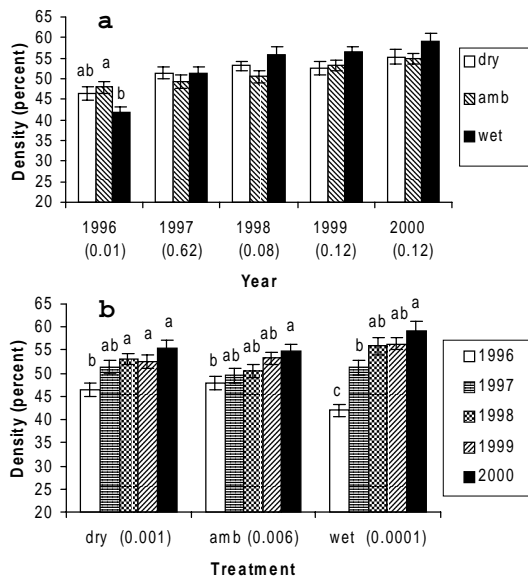


Figure 6—Mean crown densities (" s.e.m.) of sample trees for a) treatments by years and b) years by treatments. Numbers in parentheses on the x-axis are p-values from the ANOVA tests. Means with different lowercase letters, in a year or treatment category, differ at $p=0.05$ by Tukey's mean comparison tests.

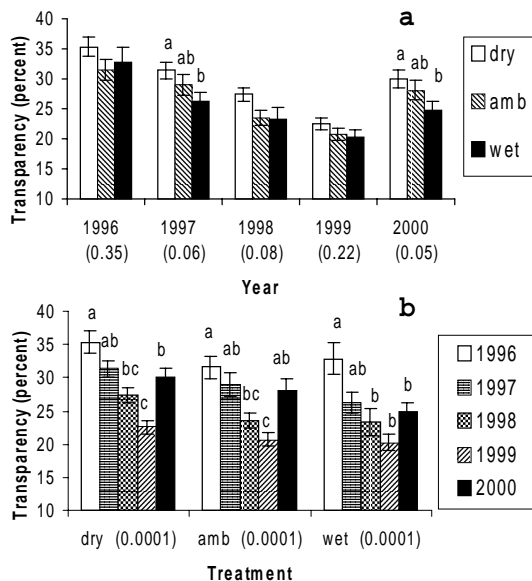


Figure 7—Mean crown transparencies (" s.e.m.) of sample trees for a) treatments by years and b) years by treatments. Numbers in parentheses on the x-axis are p-values from the ANOVA tests. Means with different lowercase letters, in a year or treatment category, differ at $p=0.05$ by Tukey's mean comparison tests.

Live Crown Ratios

Analysis revealed that the average live crown ratio on the AMB plot was greater than that on the DRY plot in 1997, but it is not clear what this means from a physiological standpoint (figure 5a). It is interesting to note that on the WET plot, there is a tendency for the average live crown ratio to decrease over time (figure 5b). This decrease is not statistically significant, but suggests a physiological

adjustment of crown length due to added soil moisture, although in the opposite direction of what might be expected. An examination of physiological variables such as water use efficiency and chlorophyll concentrations would need to be done to determine if this was a meaningful trend, and to determine what other factors might be involved.

Crown Density

Average crown density on the AMB plot was greater than that on the WET plot in 1996, but this relationship was not consistent with trends in average crown densities measured the next four years when crowns on the WET plot tended to be denser (figure 6a). Crown densities increased consistently on all three throughfall treatment plots from 1996 to 2000, and this in light of overall decreasing rainfall and soil moisture over those years (fig 6b). One might expect crowns to be less well foliated under a drying soil regime.

Crown Transparency

Tree crowns tended to exhibit less transparency, which means that there was less light visible through them, as soil moisture availability increased on the plot (figure 7a). These differences were statistically significant in 1997 and 2000. Transparency also tended to decrease on all three throughfall treatments from 1996 to 2000 as rainfall tended to decrease over the same period (figure 7b). Decreasing transparency is consistent and expected in conjunction with the consistent increases in density measured for all plots. It is interesting to note the increase in transparency on all plots in 2000, which was the third in a series of three dry years (figure 7b). It could be that an effect of three consecutive dry years is becoming evident.

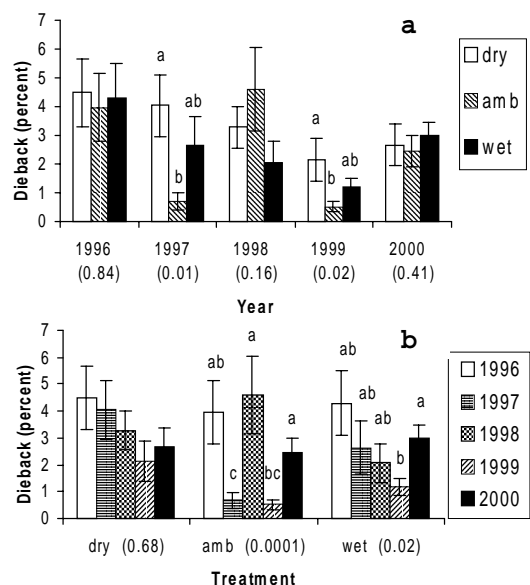


Figure 8—Mean crown dieback (" s.e.m.) of sample trees for a) treatments by years and b) years by treatments. Numbers in parentheses on the x-axis are p-values from the ANOVA tests. Means with different lowercase letters, in a year or treatment category, differ at $p=0.05$ by Tukey's mean comparison tests.

Crown Dieback

Crown dieback was quite variable across throughfall treatments over the years. In 1997 and 1999, dieback was greater on the DRY plot than on the AMB plot (figure 8a), which makes sense physiologically since drought-stressed trees should have more dieback than trees receiving adequate moisture. Dieback tended to decrease from 1996 to 2000 on all throughfall treatment plots as rainfall and soil moisture tended to decrease (figure 8b), which is opposite of expectations. Again, there is an increase in dieback on all plots in 2000, the third of three dry years.

CONCLUSIONS

The current transfer of one third of the throughfall from the DRY plot to the WET plot on the TDE is probably not sufficient to cause large enough visual differences in crown health to be differentiated using the FHMP crown rating protocol. While some crown condition responses make sense from a biological and physiological standpoint, particularly for transparency and dieback, many of the results are either too variable or are opposite of what might be expected biologically. The principal investigators of the TDE have discussed the merits of doubling throughfall displacement from one third to two thirds in an effort to increase responses of large trees to hydrologic manipulation. Early sapling mortality patterns showed more dogwood dying on the DRY plot than on the AMB and WET plots; however, the long-term pattern shows reductions of dogwood and red maple mortality on the WET plot compared to that on the Tree responses are confounded by the fact that large trees with large root systems are situated in fairly small plots in the experimental area. There is little doubt that roots of the larger trees are growing in other treatment plots, or outside the treatment area. As a result, these data need to be analyzed after having stratified them according to crown position, diameter, and perhaps species. This might reveal treatment responses not seen in the present analysis of the combined data set. More detailed regression analyses using physiological and site variables are currently underway, the results of which will be published as a chapter in a Springer-Verlag book describing all the various research efforts and current findings from the TDE site.

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FOOD RESERVES IN MOUNTAIN LONGLEAF PINE ROOTS DURING SHOOT ELONGATION

Charles H. Walkinshaw and William J. Otrosina¹

Abstract—Survival and growth of longleaf pine seedlings depends upon a well-developed root system. Soil moisture is also critical for the seedling to emerge from the grass-stage. When longleaf pine seedlings emerge from the grass stage, they grow rapidly in height and diameter. Branches are often few in number and, if present, may have low photosynthesis rates. This growth pattern is seen on all longleaf pine sites, including low fertility mountain soils. Root growth patterns on poor soils suggest that biochemical adaptations are occurring when compared to those of Coastal Plain soils. Our results show that roots of mountain longleaf pine have a normal anatomy but also have unusual amounts of starch when compared to loblolly pine roots growing during phenologically equivalent time periods. Longleaf pine roots from mountain soils appeared large in diameter and appeared to grow much nearer the soil surface than roots we observed from Coastal Plain longleaf pine. Among the variables examined to determine root food reserves, numbers of starch grains were found to be easiest to quantify. Starch grains were large in size and uniformly filled root cells. Nuclear staining served to verify the observed root cells were healthy. These results yield methodology potentially useful in assessment of health and productivity of longleaf pine.

INTRODUCTION

Longleaf pine (*Pinus palustris* Mill.) is considered as resistant or highly tolerant to many diseases and insects that adversely affect other southern pine species (Derr 1966, Mann 1969). Under some conditions, prescribed burning has been associated with increased mortality of mature longleaf pine (Otrosina and others 2000). The increased mortality is also associated with presence of certain root infecting fungi (Ophiostomatoid fungi such as *Leptographium* species and the root rot pathogen *Heterobasidion annosum* (Fr.)Bref.) not previously thought to be pathologically important in this tree species but may be indicators of ecosystem stress. This study is part of an ongoing project designed to measure and explain root mortality in longleaf pines that receive prescribed fire infrequently or have prescribed fire reintroduced after a long interval. To accomplish this goal, we are employing histological and statistical methods to identify variables in roots that are associated with this mortality. We attempt to quantitatively and qualitatively characterize fine root tissues we define as healthy; those roots having high food reserves, low mortality, and normal cortical cell nuclei. Means for histological variables we investigated can become standards to evaluate efficacy, effect, and consequences of fire and other silvicultural practices as well as to interpret other root pathological activity reported previously (Otrosina and others 2000).

MATERIALS AND METHODS

Longleaf pine saplings used in this study were approximately 10 years old and located in the Talledega National Forest (figure 1). Roots from 12 saplings undergoing rapid height growth were chosen because they must develop rapidly

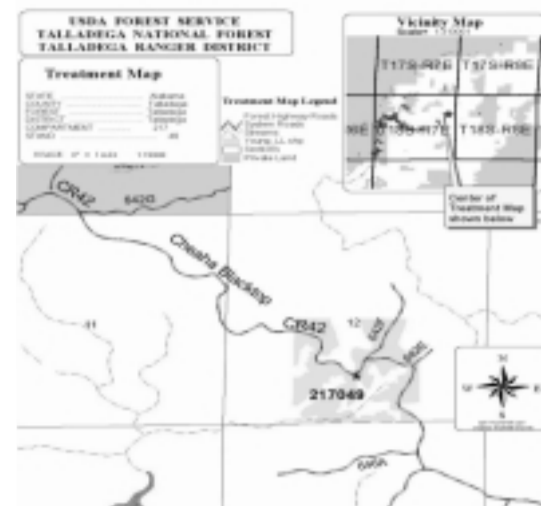


Figure 1—Location of longleaf pine saplings used in this study.

and extensively to support height growth rates of 1.0 to 2.0 meters per year. The stand of several thousand sapling longleaf pine was approximately 3.5 m in height. The randomly sampled trees ranged from 6.0 to 8.0 cm d.b.h. (diameter at breast height). Buds had not expanded at the time of sampling.

Roots were also sampled from randomly selected adult longleaf pine in northwestern South Carolina (Savannah River Site, New Ellenton SC). Trees sampled at this

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Table 1—Description of variables used in longleaf pine root histological studies

VARIABLE	P-VALUE ^a	DEFINITION
Abnormal Cambium	0.500	Cambial initials reduced in number or out of alignment. Necrotic derivations present.
Bark Formed	0.0001	Intact layer of bark cells similar to those found in the stem encompasses the root. Protects the root from injuries and microbial invasion.
Dead Roots	0.231	Cells with ruptured membranes. Tannin adhere to cell walls. Chromatin abnormal. Starch grains may or may not be present.
Large Root	0.0112	Roots more than 3 mm in diameter.
Nuclear Stain (abnormal)	0.231	Indicates degeneration (pyknosis) of chromatin.
Number Of Starch Grains	0.0189	Number of starch-containing plastids per cell viewed at a single focus per cell length at 100 to 500 diameters.
Small Roots	0.0326	Actual measurement of roots less than 3 mm.
Size of Starch Grains	0.0008	Size of starch grains scored as 1, 2, or 3 for each cell. Range in actual size was 0.5 to 4.0 microns.
Starch Use	0.0001	Starch grains 50 percent or more hydrolyzed.
Tannin	0.5393	Accumulation of excess tannin-containing cells in the cortex, rays and inner xylem.

^aFrom ANOVA that compared values for variables in roots of 12 saplings.

Table 2—Variation in starch grain number, size, and use in fine roots of sapling longleaf pines

Sapling	Number of roots	Number of grains per cell	Relative size of grains ^a	Starch use index ^a
1	21	20.2	2.67	0.048
2	14	21.2	2.78	0.071
3	23	17.3	2.30	0.087
4	15	16.3	2.40	0.067
5	16	15.1	2.25	0.125
6	14	17.1	2.50	0.214
7	13	17.5	2.08	0.231
8	19	21.3	2.68	0.579
9	14	18.1	2.43	0.0714
10	18	18.5	2.89	0.444
11	24	17.0	2.71	0.083
12	19	18.5	2.74	0.211

^aSee table 1 for definitions.

location were from unburned plots that are part of a prescribed burning study previously reported (Otrosina and others 2000). The Alabama and South Carolina locations are at equivalent latitudes and under management by the USDA Forest Service. The adult trees ranged from 25 to 35 cm d.b.h. Buds had not expanded at the time of sampling.

From both locations, roots within 8.0 cm of the soil surface were collected from the main laterals and immediately placed in formalin:acetic acid:alcohol (FAA) fixative solution (Sass 1951). After several weeks in FAA, root pieces 3-4

mm long were rinsed thoroughly with 70 percent ethanol, dehydrated, in 100 percent ethanol, paraffin embedded, and sectioned and 8-15 microns. Staining involved a number of acidic and basic dyes (Hass 1980, Horobin and Bancroft 1998, Preece 1972). See references for pertinent literature regarding detailed histological procedures.

Root tissue mortality was scored when nuclear stains were abnormal and expressed as percentage of fine roots examined. Abnormally staining nuclei appeared as grey to dull brown rather than red or blue-grey in a microscopic field of about 100 microns in radius. Other variables measured are in table 1.

RESULTS

Roots from the 12 mature longleaf pines had less starch, more tannin, and higher mortality than that of saplings:

VARIABLE	SAPLING ^a	MATURE ^a
No. starch grains	15.1 - 21.3	1.60 - 6.40
Tannin ^b	.048 - .261	0.54 - 0.90
Mortality ^b	.000 - .071	0.10 - 0.67

^a Values indicate range.

^b Proportion of roots with this variable.

Nuclei stained normally in roots from 11 of the 12 saplings and in 50 percent of the roots from adult trees. A similar result was obtained in evaluating cambial condition: 96.2 percent were normal in sapling roots and only 76.2 percent

were normal for the mature trees. Means for the roots from the 12 saplings were not significantly different for the following variables: abnormal cambium, root mortality, nuclear stain, small roots, and tannin accumulation. Also, for the saplings, variables with the largest and statistically significant differences among means occurred in size of starch grains and starch grain use (tables 1 and 2). Roots from sapling number 8 had significantly ($\alpha = 0.05$) higher numbers of starch grains (21.3) and greater use of starch (0.579) than the other root specimens. Moreover, the proportion of tannin-containing cells in roots from this tree was only 0.0526 compared to an over all mean of 0.124.

DISCUSSION

Roots of saplings appear to be models for healthy tissues in longleaf pines. They contain high numbers of large starch grains and have active nuclei. Only one root died and the proportion of roots with excess tannins was much lower compared to mature trees. Roots from the adult trees reflect a number of processes that appear to be minimal in the saplings. For example, the high numbers of dead roots in adult trees might imply a much greater turnover rate relative to the young saplings.

Thus, studies involving root metabolism interactions with silvicultural treatments should take advantage of sapling root vigor as a standard reference point for comparison. The variable, starch use, was particularly sensitive for comparing roots on different saplings. Although we did not measure the sink for the glucose that results from starch hydrolysis, large quantities of simple carbohydrates would be needed to sustain growth of the root system and for rapid top growth (1.0 to 2.0 m per year) (Allen and Scarbrough 1969). This sensitivity can also confound data interpretation as they related to site productivity and silvicultural regime, and underscores the necessity of further comparative studies.

On the other hand, the dramatically lower starch concentration in mature tree roots may imply a degree of stress and unthriftiness. This is supported by our data on the high amount of infected roots present on this site (Otrosina and others 2000). Assessment of root vigor and health by application of these standard histological procedures will contribute to evaluation of various silvicultural treatments

and their effects on forest health and productivity such as being conducted by Haywood (2000).

CONCLUSION

This study begins to address a void in our knowledge of the histological parameters that can be useful in evaluating effects of silvicultural treatments in longleaf pine and other pine species. Further comparative studies are needed over a wide range of sites, silvicultural treatments, age classes, and pathological conditions. Once baselines and key variables are established, these techniques will permit forest health assessment over wide geographic areas.

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